

# TRANSACTIONS.

- I.—The Glacial Geology of the Southern Uplands of Scotland, West of Annandale and Upper Clydesdale. By J. Kaye Charlesworth, D.Sc., Ph.D., F.G.S., Professor of Geology, Queen's University, Belfast. *Communicated by Dr J. HORNE, F.R.S.* (With One Map.)

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## I. PHYSICAL FEATURES AND GEOLOGICAL STRUCTURE.

The present paper embodies the results of an investigation into the glacial phenomena of the Southern Uplands of Scotland, west of Annandale and Upper Clydesdale.

The literature dealing with the glaciation of this extensive region is very meagre. Apart from the *Memoirs of the Geological Survey of Scotland*, only a few and scattered papers and occasional references bear upon the subject. These will be noted in the course of the paper as occasion arises.

Some idea of the physical features of the area will be gathered from the accompanying map. This shows that the hills trend north-east south-west and are divided into separate clusters by three transverse depressions. The most easterly of these is the line of Annandale and Upper Clydesdale, the middle one, Nithsdale, while the westerly one follows the valleys of the Ken, Carsphairn Lane, and Lower Doon. East of Nithsdale rise the Lowthers, culminating in Green Lowther (2403);\* other hills are Queensberry (2265) and Cairn Table (1944). West of the Nith the mountains culminate in Cairnsmore of Carsphairn (2614). West of the Ken lie the twin ranges of the Rhinns of Kells, including Corserine (2668), Meaul (2280), and Meikle Millyea (2446); and the Merrick hills, with Shalloch on Minnoch (2520), Tarfessock (2282), Kirriereoch (2562), and the Merrick (2764), the greatest altitude of

\* The figures in brackets indicate altitude of the hills in feet.

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south Scotland. These ranges trend roughly north and south, and are separated by the broad depression which contains the lochs of Doon and Dee; it is drained northward by the river Doon, and southward by the Cooran Lane, the head waters of the river Dee. To the south these parallel ranges are cut off by Glen Trool and the Dee valley from the hills culminating in Lamachan Hill (2349), Larg Hill (2216), Curlywee (2212), and Millfore (2146), and these again from Cairnsmore of Fleet (2331) and the adjacent hills by the deep valley of the Palnure Burn.

On the west, the Merrick, Lamachan Hills, and Cairnsmore of Fleet fall steeply to the Water of Cree and the low moorland, which stretches away to Luce Bay and the Rhinns of Galloway; Beneraird (1435) rises out of this peneplain. Eastward, this coastal plain extends along the northern shores of the Solway Firth; Annandale, Nithsdale, and the Ken valley open on to it, and Criffell (1866) and Bencairn (1250) rise steeply from it.

The region consists of Ordovician and Silurian slates, grits, and greywackes, with bands of chert, the whole striking roughly north-east south-west. Into these have been intruded several granite masses, the Dee granite, flooring the depression extending from the south of Loch Dee to the shores of Loch Doon and between the Merrick and Kells ranges (which are built of the indurated Ordovician rocks of the contact zone), the Cairnsmore of Fleet granite stretching eastward from this hill to the banks of the river Ken, south of New Galloway; the Criffell granite forming Criffell and underlying the country extending to the south of Dalbeattie and to within a few miles of Kirkcudbright; the Cairnsmore of Carsphairn granite forming this hill; the Spango granite, west of the Spango hills. Smaller masses occur near Creetown, in the Afton Water and at the Knipe, the last two being situated south-east of New Cumnock, while the Mull of Galloway granite lies a few miles north-west of this head.

A strip of Carboniferous sandstones, shales, fireclays, and coals, and of Triassic sandstones and conglomerates, borders the western and southern shores of Loch Ryan, while Carboniferous rocks skirt, at intervals, the northern shores of the Solway Firth. These rocks also underlie the depression of Thornhill and form the Sanquhar coalfield. Sandstone, marls, and breccias cover considerable areas in Nithsdale and Annandale.

## II. GENERAL CHARACTER OF THE GLACIATION.

The lines of ice-flow over the regions are clearly indicated; in the uplands they are given chiefly by the striæ, in the plains and valleys by the drumlins. As these features are inserted on the accompanying map, but few details need be given. Striæ are in general by no means abundant. They have rapidly disappeared from weathered surfaces, but are finely displayed on recently bared rock-surfaces, as in quarry and road excavations. They are relatively rare on granite and the lower Palæozoic slates, more especially when these are thinly cleaved or bedded and highly inclined. Instances of terminal curvature were not infrequently observed and were noticed by earlier workers.\*

During the early phase of glaciation, all the higher hills including Criffell and the Lamachan Hills doubtless nourished independent glaciers. At the maximum stage, however, the ice-centres lay over the higher mountains which to-day form the main watershed. Toward the west the ice-shed coincided with the Merrick and Corserine and included the wide depression between those hills, covering the site of Loch Enoch and the watershed between the Cooran and Gala Lanes. It was prolonged eastward in the Cairnsmore of Carsphairn and adjacent hills and in the Lowthers.

\* E.g. J. SMITH, *Trans. Geol. Soc. Glasgow*, xi, Suppl. (1898), p. 49.

The ice radiated from Corserine and the Merrick\* down the larger valleys, *e.g.* Glen Trool and the valleys of Dee and Doon. It proceeded over the Lamachan and neighbouring hills, as is conclusively proved by the striations and by the occurrence of boulders of the Loch Dee granite on the very summit of these greywacke mountains. On the north the ice swept down the valley of Loch Doon, while parallel flows proceeded to the north and north-west from the hills between Cairnsmore of Carsphairn and New Cumnock, submerging Enoch Hill (1865), streaming down the valleys of the Afton Water and the Nith, and over Cairn Table and the Hagshaw Hills. The Clyde carried much of the ice from the Lowthers and Leadhills. This ice overrode Tinto and the intervening hills, transporting characteristic erratics from the Southern Uplands to an uncertain yet considerable distance into the Central Valley. Thus fragments of the white Cairn Table sandstone are strewn abundantly over the hills to the north and north-west, *e.g.* over those around the Douglas and Muirkirk coal basins and the Hagshaw Hills.† They have also been traced eastward as far as the Pentland Hills.‡

The existence in south and central Ayrshire of a zone some 20 odd miles in width, strewn with erratics from north and south,§ shows that this area was the meeting-place of the Highland and Southern Upland glaciers. Under the influence of the powerful Highland ice, the glaciers streaming northward from the Southern Uplands, more especially from the region of the Doon, were deflected through west to south-west and caused to flow coastwise in south Ayrshire; striæ run parallel with the coast on the flanks of Pinbane Hill, at Downan Point, and south of the Stinchar fault.|| This curving of the lines of ice-flow is shown by the striæ south of Straiton and along the valleys of the Stinchar and Girvan Water, and by the curving along the same course of the main track of the Loch Dee granite erratics. This ice, laden with countless boulders of the Dee granite and erratics from the sedimentary and igneous rocks of Ayrshire, swept off this coast and on to the Rhinns of Galloway, there depositing its material, with fragments of marine shells and Cretaceous flints dredged from the floor of the sea. Over the site of Luce Bay it became confluent with the ice which was flowing in a general south-westerly course over the Machers of Wigtownshire from Glen Trool and the Merrick Hills.

The trend of the ice north of Wigtown Bay was, in the main, north-south, *i.e.* parallel with the axes of the valleys, *e.g.* the Grennoch, the Grobdale Lane, and the Little Water of Fleet. South of Gatehouse of Fleet the direction was about S. 30' W., as shown by the trend of the low, elongate drumlins and the trains of felsite boulders from the north-east of Kirkcudbright.

The Ken was glaciated roughly parallel with its course; thus the striæ north-west of Castle-Douglas bear south-east, those toward the Tarff and Fleet south or west of south, in the region of Twynholm and Borgue south or south-south-west, near Kirkcudbright and Auchencairn south-east, and in the valley of the Urr south-south-east.

The ice along the contact of the glaciers of the Nith and Ken swept over Criffell and the adjacent hills, for, though slates were not suited to transport, small pieces of these rocks, together with boulders of coarse grits and other rocks from the Silurian country to the north, were carried into the Criffell valleys and even to the summits. Lower Palæozoic erratics lie scattered over the granite country south of Castle-Douglas. These hills, *e.g.* Bengairn, are rounded from the north or north-west, and the vertically jointed granite has been bevelled in this direction. In Nithsdale there was a general south-east transport of drift.

\* This was recognised by W. JOLLY, "On the Evidence of Glacial Action in Galloway," *Trans. Edin. Geol. Soc.*, vol. i (1868), p. 161.

† *Mem. Geol. Survey*, Sheet 23 (1873), p. 45.

§ J. GEIKIE, *Great Ice Age*, 3rd ed. (1894), p. 828.

‡ *Ibid.*, Sheet 15 (1871), p. 40.

|| *Mem. Geol. Survey*, Sheet 7 (1869), p. 14.



They are abundant in the Ken valley, north of Smeaton Bridge, and in its feeders the Castlefin Water and the Black Mark Burn. They decrease rapidly along the Ken, becoming extremely rare in the south. None were found south-east of the Ken, below Balmaclellan, or thence to the Urr.\* They were encountered in goodly numbers over Stroanpatrick, Culmark, Fingland, and Lochlee Hills, but occur singly and at considerable intervals as traced to the south-east.

North of the outcrop they are found strewn over the valleys and hills to the summit of Enoch Hill, but become rapidly rarer as followed east of this. They can also be clearly traced toward Dalmellington, where they merge into the stream of granite boulders from Loch Doon. They occur at least as far north as the neighbourhood of Ochiltree.† Beyond this it has not been attempted to follow them. In short, they occupy a relatively narrow strip of country, averaging possibly some 10 miles in width and trending north-west south-east. This distribution would appear to be due to the situation of the granite outcrop on that part of the ice-shed from which glaciers flowed on more or less parallel courses, so permitting of little spreading.

The Spango granite erratics were carried to the west into the valleys of the Gwelt, Glenmuir,‡ Gass, and Garpel Waters, and into the higher reaches of the Ayr and Greenock Water.§ The writer found them in the Nith valley, well to the north of New Cumnock. They have been traced across the Douglas Water and over the hills south and north of the Douglas coal basin,|| including the Hagshaw Hills,¶ and north-east of these to an altitude of 1200 feet.\*\* They have also been observed at Lesmahagow.††

To the south-east they occur plentifully in the Spango Water‡‡ and its tributaries, and between this valley and the Crawick Water, e.g. in the Spothfore and Kiln Burns. They are abundant in the Crawick Glen, whence they are traced to its confluence with the Nith, and even as far south as Enterkinfoot. A few were transported up the Cog Water to an altitude of 1060 feet,§§ and up its tributary the Glensalloch. They were also carried sparingly up the Wanlock Water for a distance of 3 miles,||| and up its tributary valleys, e.g. the Deutercleuch, Glenbuie, and Clacklieth Burns, to an altitude of 1100 feet.¶¶ An occasional boulder was discovered in Glendyne,\*\*\* a tributary of the Mennoch Water, and in Glemishaw,††† to an altitude of 600 feet. Mr J. SMITH found a large boulder at an altitude of 1340 feet on the railway east of Leadhills. This boulder which he refers‡‡‡ to the Loch Doon granite is doubtless of Spango granite. There is no Loch Dee granite in this district (see above) as Mr J. SMITH frequently maintained,§§§ nor any trace of the Knipe or Afton Water granites, as he also asserted.|||| To the east of the outcrop these boulders occur in the Duneaton Water and its tributary the Sherifcleuch Burn,¶¶¶ and up the Snar Water to an altitude of 940 feet.\*\*\*\*

The dispersal to all points of the compass of boulders from this outcrop, and the occurrence of erratics of Lower Palæozoic greywackes, etc. upon it, indubitably prove an oscillation of the

\* *Mem. Geol. Survey*, Sheet 9 (1877), p. 37.

† *Ibid.*, xi (1899), p. 256.

‡ *Mem. Geol. Survey*, Sheet 15 (1871), p. 38.

§ *Ibid.*, p. 45.

|| *Ibid.*

||| *Mem. Geol. Survey*, Sheet 15 (1877), p. 38.

¶¶ J. SMITH, *Trans. Geol. Soc. Glasgow*, xi (1899), p. 256.

†† J. SMITH, *Proc. Liverpool Geol. Soc.*, vii (1900), p. 485.

‡‡ *Ibid.*, p. 497.

§§ *Ibid.*, pp. 485-90.

||| J. SMITH, *Proc. Liverpool Geol. Soc.*, vii (1900), p. 485.

† *Of J. SMITH, Trans. Geol. Soc. Glasgow*, xi, Suppl. (1898), p. 41.

§ *Ibid.* (1898), p. 58.

¶ *Ibid.*

‡‡ J. SMITH, *op. cit.*, p. 256.

§§ J. SMITH, *Proc. Liverpool Geol. Soc.*, vii (1900), p. 487.

¶¶ J. SMITH, *Proc. Liverpool Geol. Soc.*, vii (1900), p. 486.

§§§ *E.g., ibid.*, p. 486.

¶¶¶ J. SMITH, *Trans. Geol. Soc. Glasgow*, xi (1899), p. 256.



ice. The southward dispersal of these erratics is due to the pressure of the Highland ice from the north, and shows a thrust into the Southern Uplands such as is nowhere else in this region even approached. That this influence should be felt so far south is due to the fact that Upper Clydesdale led away to the north-east the southern ice from the Lowthers, etc., while the ice from around the Nith was naturally directed to the north-west, a weak area arising thereby between these valleys. A contributory cause was the southward opening of most of the valleys tributary to the Nith, so that their glaciers went to strengthen the Nith Glacier.

The granite erratics from the Afton Water and Knipe outcrops are found over the New Cumnock area and over the Carboniferous tracts to the north.\*

The distribution of the boulders from the Criffell granite is chiefly outside the area under review. In the Southern Uplands they are strewn over a relatively small area; they were carried to the south-west to Kirkcudbright and Kirkcudbright Bay, to the south-east to the Solway, and to the east to Langholm, Canonbie,† and certainly as far north as Penton in the Liddell valley.

Numerous other types of rocks were used in the course of this research, of which a few only can be noticed here. The felsites north of Kirkcudbright are plentiful as erratics to the south of the outcrop, but were traced westward to the country south of Gatehouse of Fleet, and eastward as far as Orroland. Felsites are widely, though sparsely, distributed over other regions, *e.g.* in the valleys of the Stinchar and Girvan Water, over all the country extending west and south-west from Straiton, and in the Rhinns of Galloway. These were derived from the numerous outcrops in south Ayrshire, reinforced doubtless in the drift of the Rhinns of Galloway by contributions from the Arran felsites.

The hyperites form ill-defined fans. In the Machers of Wigtownshire these are spread out to the south and south-west from the outcrops west of Newton-Stewart, north-west of the Kirk of Mochrum, and east of Auchenmalg Bay respectively.

Boulders from the basalt dykes of the Upper Clyde and its tributaries are found in varying quantities in the drifts of the valleys of this area, *e.g.* the Clyde, the Duneaton, Elvan and Glengonar Waters, and those of the intervening hills. They indicate a carry over to the north or north-east. The occasional boulders of basalt in Moffatdale, below Moffat, were derived from the dykes of this area. Cherts from the lower Palæozoic rocks were frequently found as small fragments in the drifts. They are fairly plentiful in some areas, *e.g.* near Glenluce, west of Newton-Stewart, east of Parton, in the Clyde below Crawford, and the Stinchar below Barr. In all cases their distribution is confirmatory of the direction of ice-flow given above. The Queensberry grits in Dumfries are found, in general, to the south-east of the outcrops.

No erratics of the Carboniferous sandstones and conglomerates bordering the northern shores of the Solway, east of Kirkcudbright Bay, were noted to the north of the outcrop; they were carried southward into the Solway.

The most complex drifts of this region are to be found in the Rhinns of Galloway. There though good exposures are relatively few, the following erratics were identified; granite of Loch Dee, Arran, and possibly Cairnmore of Fleet; felsites from south Ayrshire and Arran; New Red Sandstone and breccias from Loch Ryan and probably also from Arran; basalts and dolerites from the sills and lavas of Ayrshire, and much gabbro and peridotite from the Girvan area; Old Red Sandstone and Carboniferous sandstones from Ayrshire; pieces of shale and coal the latter especially in washed and sorted sands and probably derived from the western shore

\* *Mem. Geol. Survey*, Sheet 15 (1871), p. 38.

† D. MILNE HOME, *Trans. Roy. Soc. Edin.* (1844), p. 463.

of Loch Ryan; black chert, vein quartz from older rocks, with schist, gneiss, and quartzite from the Dalradians; the paisanite of Ailsa Craig; Cretaceous flints, and, more rarely, chalk and fragments of marine shells.

The paisanite of Ailsa Craig, in both its coarser and finer varieties, was first detected in the drifts along the coast, a few miles north of Ballantrae. Though its erratics occur here only as rare and small pieces, they become increasingly large and plentiful as the coast is followed southward toward Loch Ryan. In the Rhinns of Galloway they were found in great profusion and as boulders ranging up to 1 foot in diameter. They were also discovered in the drifts east of Loch Ryan and of the mouths of the valleys draining westward into the loch. They occur in great abundance in the moraines, outwash fans, and raised beaches separating Loch Ryan from Luce Bay.

Cretaceous flints have almost the same distribution. Occasional flints make their appearance in the drifts about Ballantrae, but become larger and more abundant as the drifts are examined to the south. They occur along the eastern shore of Loch Ryan with occasional small chalk fragments, and in their greatest numbers and largest size in the drifts of the Rhinns of Galloway. They are present in the modern and raised beaches round the head of Luce Bay and in the sandhills of Torrs Warren, etc.

The flints of the beaches have doubtless been derived from the waste of the drifts. Mr J. SMITH supposed the flints of the drifts to have been transported from Ireland by seaweed during the glacial submergence.\* It is highly improbable that they were transported from north-east Ireland either by sea or ice. They were doubtless dredged by the Clyde ice from Cretaceous outcrops on the sea-floor between Arran and the Rhinns of Galloway, and transported with the marine shells and Ailsa Craig paisanite by the southward-moving ice-sheet.

T. M. READE† noted shelly boulder clay in the banks of Byne Hillburn (2 miles south of Girvan) and, with J. W. DAVIES, between Benane Head and Girvan. Shells were early recorded from the drifts of the Rhinns of Galloway,‡ and by J. C. MOORE from those along the western shore of Loch Ryan.§ The writer discovered them in the drifts all over the Rhinns, and in those along the eastern shores of Loch Ryan, especially in the associated sands and gravels and in the stratified drifts to the south of this bay. Boulders of Arran granite have, in general, a similar distribution. They were noticed in the neighbourhood of Ballantrae, and by Dr D. FORSYTH|| at Girvan. They also occur over the Rhinns of Galloway and along the eastern shore of Loch Ryan.

The distribution of the boulders from Arran and Ailsa Craig, and of the shells and Cretaceous flints, is corroborative of the conclusions already outlined as to the lines of ice-flow over this part of Wigtownshire and south Ayrshire.

### III. THE RETREAT.

Almost the sole evidence as to the mode of retreat of the Southern Upland ice in the region which was investigated is furnished by moraines and outwash fans, which are finely developed in connection with all the major glaciers. Marginal drainage channels are, with but few exceptions, quite absent.

It is proposed to describe briefly the moraines of each valley in their order of age, and to take the glaciers in turn, beginning with the Cree Glacier, and working round in a counter-clockwise direction. While minor correlations will be simultaneously attempted, the larger

\* *Trans. Geol. Soc. Glasgow*, vi (1880), p. 185.

§ *Quart. Journ. Geol. Soc.*, vi (1850), p. 388.

† *Geol. Mag.* (1896), p. 545.

‡ *Mem. Geol. Survey*, Sheet I (1872), p. 9.

|| *Trans. Geol. Soc. Glasgow*, vii (1883), p. 251.



correlation of the several stages of recession in the different glaciers will be postponed until the conclusion of the description.

The position and distribution of the moraines are shown on the map.

As references will throughout be given to descriptions of those features which have been made by earlier workers, attention will be directed in the following discussion to the location of the moraines; details of their form, composition, and structure will be omitted.

### 1. *The Cree Glacier.*

The Cree Glacier was fed chiefly by the smaller glaciers streaming from the western valleys of the Merriek range, with considerable contributions at one stage of the ice from the hills of Lamachan and Cairnsmore of Fleet, which lay on its eastern flank.

(a) *The Monreith Series.*—The most southerly moraines of this glacier are the sand and gravel mounds observed in Monreith Park, west of Monreith, at the camp of Laggan, near Carleton Fell,\* and at Drumpail Bridge, approximately 5 miles north-east of Glenluce. The sands and gravels in the Water of Luce, at New Luce, may be morainic and, if so, belong most probably to this stage when a glacier was thrust southward from the region of Glenwhilly.

(b) *The Kirkcowan Series.*—A fine moraine of water-worn sands and gravels crosses the main road,  $1\frac{1}{2}$  miles north-west of the Isle of Whithorn. It runs from Prestrie to near Arbrack,† and was formed by ice, here relatively thin, deploying over Wigtown Bay and slightly encroaching on its shores. This moraine can be traced at intervals to the west of Wigtown Bay, occurring at Portyerrock,‡ north-west of Port Allan, in the grounds of Galloway House and in places between Sorbie, Garliestown, and Kirkinner; at Kirkinner it is very well developed. Though the northern continuation is lost beyond here there are grounds, as explained below, for believing that its line is roughly coincident with the course of the River Bladnoch as far as Kirkcowan, in which district the moraines are again beautifully displayed. To these belong the ridges and mounds north-west of Kirkcowan,§ and those about Mark Shennanton and Bladnoch Bridge. They sweep from Kirkcowan to Drumbuie and east of Barnaigh to Carsebuie. A slightly later line is given by the mounds running approximately east of Kirkcowan and west of Shennanton. Still later ridges marking the ice-edge were found, one situated near Bladnoch Bridge, a second one running through Mark Shennanton and north of the railway. All these features occur to the east or south-east of Culvennan Fell. Sweeping round its northern side the moraine is further developed in the sand and gravel mounds of West Culvennan, extending round Black Loch and westward as far as the road north of the loch. This corresponds with the outermost Kirkcowan moraine. A slightly later stage, of the same age as the Shennanton moraine, was observed east of the school. Though careful search was made on the moors between here and Barrhill, further certain trace of the moraine was not discovered.

(c) *The Newton-Stewart Series.*—A retreat of considerable magnitude and of an apparently uninterrupted nature carried the margin of the ice to another line of halt which is as sharply defined as the preceding one. The moraine of this halt is best displayed to the west of and about Newton-Stewart, where there is developed a fine kettle-moraine whose outwash fan stretches southward down the Cree. The mounds and ridges were found at Minnigaff and at Broom Isle. They are best shown, however, along the road and railway

\* *Mem. Geol. Survey*, Sheet 2 (1873), p. 9

† *Ibid.*

‡ *Ibid.*

§ *Ibid.*, Sheet 4 (1878), p. 21.



running westward from Newton-Stewart to Merton Hall and Black Park, whence they trend somewhat west of north for a couple of miles. A later ridge runs parallel with this about half a mile to the north. Later moraines, all of this stage, are concentric through Challoch and Boreland, while a still later crescent passes through Castle Stewart. To this series belong the sand and gravel mounds at The Knowe and the one west of Loch Dornal. Over the intervening tracts to the south this moraine was not detected, nor was any trace of it found to the west till Barrhill was reached.

During the retreat from the Kirkcowan to the Newton-Stewart stage, the connection with the ice from the Cairnsmore of Fleet hills was severed. This ice formed two glaciers, the one flowing along the Moneypool Burn to Creetown, the other along the Palnure Burn. The moraines of the first glacier were noted near Creetown Station and about  $2\frac{1}{2}$  miles north-east of this on the moors near Clanery; they also occur near the Culcronchie viaduct\* and to the west and north-west of this place. No moraines were observed in the Palnure Burn in connection with the second glacier, except to the north of Palnure itself, but a series of mounds were mapped in the valley entering the Cree, about 1 mile east of Newton-Stewart. They swing across the valley from Larg and also north of the 40 and 39 mile-stones respectively. It is quite possible that these glaciers at an earlier part of this stage either extended out over the shallows of Wigtown Bay, or that their advance was checked, just beyond the mouths of the valleys, by the waters of the raised-beach sea and the melt-waters from the ice receding up the Cree. Instances of rivers crossing the front of glaciers and checking their further advance have not infrequently been observed, e.g. by W. H. WORKMAN in Kashmir,† and by H. F. REID in Alaska.‡

The Penkill Glacier with its roots in the large corries on the southern flanks of Larg and Lamachan Hills was confluent with the Cree Glacier at the time marked by the outermost Newton-Stewart moraines. The retreat which carried the snout of the Cree Glacier to the Challoch moraine led to the separation of the Cree and Penkill Glaciers. The Challoch moraine is represented in the Penkill valley by the moraines which cross the valley above Queen Mary's Bridge and near Cumloden Cottage, passing on to its northern slopes near Garlie Wood and Glenshalloch.

(d) *The Minnoch Series*.—A further apparently quite continuous retreat and one of long duration was finally brought to a halt, and a series of morainic mounds and ridges, at very small intervals, mark the later retreat. These moraines constitute the Minnoch stage. This magnificent series, the "sea of mounds" of W. JOLLY, span the wide valley of the Minnoch Water as far south as Glencaird and to within a short distance of the confluence with Glen Trool. They were formed along the edge of the ice which was fed by glaciers issuing from the deep U-valleys running westward from between the Merrick and Shalloch on Minnoch. The ice to the north of Garwall Hill was thrust westward over the site of Loch Moan into the broad depression drained by the upper Water of Cree. Here also the moraines are finely displayed. They extend far west to Black Loch, in the area of the Crammoch Burn, and curve from Loch Crongart in the direction of Black Claughrie, in their further course following the side of the hill called Standard. They then pass in between this hill and that of Knapps, skirting the flanks of the hills to the north-east and near Rowantree School. They are beautifully shown around Loch Moan, where they merge into those in the Minnoch Water. There were, therefore, two lobes separated by the mass of Garwall Hill. The waters of Loch Moan and Kirrieroch are held up by these moraines.

\* *Mem. Geol. Survey*, Sheet 4 (1878), p. 22.

† *Zeitschrift für Gletscherkunde*, vi (1912), p. 103.

‡ *Geogr. Journ.*, xxxi (1908), p. 32.

The Minnoch stage is also represented in Glen Trool and in its tributary valleys which enter from the north. In Glen Trool itself, moraines were observed only at the lower end of Loch Trool for, apart from certain doubtful lateral moraines above the shores of the lake, any morainic mounds must now lie submerged beneath its waters.

A large block moraine occurs at the mouth of the Garland Burn, and a similar one, probably of the same age, in the lower part of the Buchan Burn. In this valley moraines were noted, at intervals, to above Culsharg, where a fine series is developed. In the Garland Burn beautiful morainic mounds were mapped at the western end of Loch Valley, and again  $1\frac{1}{2}$  miles south of this. These moraines were noticed by W. JOLLY.

(e) *The Corrie Series*.—The Corrie moraines of the glaciers which during the earlier phases fed the Cree glacier were noted in the Merrick and Lamachan Hills and in Cairnsmore of Fleet.

### 2. *The Fleet Glacier.*

The Fleet Glacier was nourished by the snows precipitated on the high fells of Cairnsmore of Fleet.

(a) *The Gatehouse Series*.—A number of morainic mounds and ridges curve from the hillsides into the valley of the Fleet over a stretch of almost 4 miles above Gatehouse of Fleet. Over the floor of the valley they rise from an extensive fluvio-glacial terrace which inclines gently seaward and to a certain extent masks the moraines.

At the stage represented by these features the ice from Cairnsmore of Fleet extended in the direction of Creetown and deposited the moraines about Culcronchie which have been already discussed in connection with the Cree Glacier.

(b) *The Big Water of Fleet Series*.—In the Fleet valley no other moraines were observed below Upper Rusko Cottage. Northward from here, however, over the wide depression extending to Gatehouse of Fleet Station and to the upper reaches of the Big Water of Fleet\* and the wide Cullendoch Moor, there is displayed a magnificent series of concentric mounds and ridges, crowded closely together and associated with an occasional esker ridge. The small morainic mounds about 1 mile east of Craigwhinnie probably represent the moraine of a small Corrie Glacier which was formed on the Fell of Fleet.

(c) *The Corrie Series*.—These moraines are well developed in the corries east of Cairnsmore of Fleet.

### 3. *The Ken Glacier.*

The growth of the Ken Glacier was due chiefly to ice from the Rhinns of Kells, Cairnsmore of Carsphairn; and a large affluent streaming along the valley of the Dee from the eastern flanks of the Lamachan and Merrick Hills.

(a) *The Southwick and Twynholm Series*.—The earliest stage in the Ken valley is represented by the morainic ridges running as a well-marked belt along the lower hill flanks east and north-east of Dalbeattie. They extend more or less continuously from near Breconside (N.E. of Kirkgunzeon) by Glaisters, Tarkirra, Bargrug, and Loch Fearn, where they are magnificently developed, and round Barclosh hills to Aucheninnes Moss† (E. of Dalbeattie). Farther south this stage has not been detected. To a somewhat earlier phase belong the morainic mounds south of this, e.g. those near the source of the Glaisters Burn in the March Burn, and those found about 600 feet above sea-level along the western side of Bail Hill.‡

\* *Mem. Geol. Survey*, Sheet 4 (1878), p. 22.

† *Ibid.*, Sheet 5 (1896), p. 35.

‡ *Ibid.*, p. 36.



Pieces of what appear to be the same moraine are the mounds of Orroland, at an altitude of about 250 feet, at Rascarrel, those on the hillside north-east of Upper Hazelfield, and the low, gravelly mounds east of Drumgans, all in the region south-west of Auchencairn. At this stage the ice appears to have fanned out over the low coastal plain south of Dalbeattie, between Screel Hill and the western and lower flanks of the Criffell mass; its front was then thrust slightly out over the Solway Firth. Lakes were held up at this stage in the depressions about Beeswing; the drainage escaped by the Glensone Burn and by the valley falling north-eastward from Lochanhead Station.

The numerous morainic mounds, situated south of Glenapp and laid down by ice retreating northward along this valley, belong here, as do also the sands and gravel mounds east and north-east of Twynholm, those near Tarff Station, extending with outwash materials as far as Ringford, and finally an occasional mound in the vicinity of Kirkcudbright.

No other moraines of this stage were observed along the western side of the Ken, for in this region the ice was confluent with that from the west and was united with it to form a large and broad Piedmont glacier, spread out to the south over the coastal plain. On the east, this ice was confluent with the Nith Glacier over the country extending north of the hills which lie about 4 miles west-north-west of Maxwelltown.

(b) *The Laurieston and Crossmichael Series.*—The next stage is marked by the magnificent series of sand and gravel mounds and ridges, which extend, with their outwash fans along the Tarff Water, from New Galloway Station to south of Laurieston and along the valley of the Ken from the neighbourhood of Parton Station to Castle-Douglas. They are well displayed on either side of the valley, as at Crossmichael, and are widely distributed over its broad floor. Near their southern limit at Castle-Douglas they are superimposed upon true drumlins.

The eastern edge of this glacier skirted the hillside east of the Urr Water. From the margin, tongue-like projections were thrust into most of the larger valleys. Thus over a stretch of almost 2 miles the moraines span, at short intervals, the valley running eastward from Loch Urr, while others occur along the Old Water,\* south of Craigenputtock, at the head of the Knarie Burn, south of Auchenhay Hill, and along the western slopes of the Largenlee Hill. Moraines and outwash material also occur in the valley of the Urr, below the old bridge of Urr, ranging in altitude to more than 250 feet above sea-level.

At this stage the ice issuing from the region around Loch Dee was still confluent with the glaciers from Cairnsmore of Fell and Fleet, and these again with the western flank of the Ken Glacier about Stroan Loch.

(c) *The Carsphairn Series.*—In the Carsphairn district there is displayed one of the finest series of moraines to be found in Galloway.† They have been traced as far south as Glenhowe, Strangasse, and Millquater‡ in the Ken valley, and less certainly to near Carlston Castle about 2 miles farther south. They set in strongly  $1\frac{1}{2}$  miles above the Deugh Linn (Tinkler's Loup), whence they extend, thickly dotted over the ground, as far north as Drumjohn and, as on the south, irregularly and at greater intervals to the flanks of the hills north-west of Lamford and to wellnigh the eastern shores of Loch Doon. These countless mounds were heaped up along the receding edge of the glacier proceeding from Meaul and Cairns-garroch along the Garryhorn on the west, and that flowing along the Deugh and its feeders from the Cairnsmore of Carsphairn hills on the east. They can be followed up the Garryhorn as far as Woodhead Lead Mines. On the east, they were mapped behind the Craig of

\* *Mem. Geol. Survey*, Sheet 9 (1877), p. 39.

† *Mem. Geol. Survey*, Sheet 9 (1877), p. 41.

‡ D. FORSYTH, *Trans. Geol. Soc. Glasgow*, ix (1892), p. 378.



Knockgrey and at several places along the Deugh, *e.g.* above the confluence of the Benloch, about Knockingaroch and near Waterhead.

To this series also belong the moraines in the Ken, above the High Bridge of Ken, *e.g.* those at Blackmark, the ridge running from Culmark to near Stroanfreggan and those which curve from the hillside, west of Stroanfreggan, to the south of Newmill of Oldhouse, past Muirdrock Wood, to the hillside 1 mile north of this. Later mounds were noted south of Craigengillan Burn, in the Polhie Burn, near Moorbrock, and at Strahannah in the Water of Ken.

In the valleys leading eastward from the Rhinns of Kells the corresponding moraines are but imperfectly developed; they occur singly above Largmore in the Garroch Burn and below Dukieston in the Polharrow Burn.

East and south-east of the Fell of Fleet this phase is represented by the relatively poor but easily recognisable moraines in the valley of the Grobdale Lane, where they extend as far south as Darngarroch, and in the valleys of Loch Lane and Little Water of Fleet, south of the railway. Here also belong the moraines in the valley of the Glengainoch Burn, west of Auchenhay Hill, in the Dee valley north-east of Shaw Hill, and those along the southern shores of Loch Skerrow, on the northern flanks of Airei Hill and east of Stroan Loch.

The glaciers converging from the north and south on Loch Dee flowed eastward along the Dee and westward into the head of Glen Trool. Their moraines are doubtless of this age. They include the very large ridges spanning the Dee, about  $1\frac{1}{2}$  miles east of Loch Dee, the mound 2 miles east of Craigenallie, and the moraines noted at intervals in the Glenhead Burn descending westward from Loch Dee into Glen Trool. With these are to be correlated the moraines near Davy's Holm and those west of the Cooran Lane, *e.g.* east of Craiglee and near Snibe Hill.

(d) *The Corrie Series.*—The corrie stage of this glacier includes the moraines in the Rhinns of Kells, Cairnsmore of Carsphairn, Fell of Fleet, and Lamachan Hills.

#### 4. *The Nith Glacier.*

(a) *The Kirkbean Series.*—Sand and gravel mounds were observed about Kirkbean\* and Mainsriddle. Poor moraines occur along the hillside between Torthorwald and Ruthwell Station, whence they continue to the east and south-east and appear to become confluent with the Cummertrees moraine of the Annan Glacier.

(b) *The Dumfries Series.*—Enormous kettle-moraines of typical form and composition, and up to 1 mile in width, are flung across the wide valley of the Nith about Dumfries. The outermost runs in a big curve from near Duncrow, by Locharbriggs Station to Dumfries; this town is largely built upon it. A later and less well-developed feature curves from the hillside north-east of Dalswinton, by Kirkton, to Lincluden House,  $1\frac{1}{2}$  miles north-east of Dumfries toward the western side of the Nith valley. The outwash from these moraines extends southward down the Nith and merges into the raised beach.

The prolonged halt which these moraines indicate was followed by an uninterrupted recession, during which the great composite Nith Glacier was dissolved into two glaciers, flowing respectively along the Nith and Cairn Water; the one retreated in the direction of Thornhill, the other of Moniaive.

(c) *The Cairn Water and Closeburn Series.*—The glacier in occupation of the Nith

\* *Mem. Geol. Survey*, Sheet 5 (1896), p. 76.

valley, below Thornhill, laid down a series of sand and gravel moraines which begin as far south as Friar's Carse and can be followed at intervals along the Nith to Blackwood. Here they skirt the hillside from Gracefield to Auchenage and from Bourtree Hill across the Nith, whence the ice hugged the flanks of the hills as far north as Heathery Dean; the melt-waters escaped by the valley south of this into the Claughrie Burn. Still further to the north, the ice deposited the moraines which were observed by Professor W. BUCKLAND.\* Here, as he noticed, a long gravelly moraine stretches nearly across the valley from which the Dolland Burn descends to fall into the Crichton Linn. Another moraine skirts the western side of the valley at an elevation of 500 feet from east of Closeburn to Auchenage. A later one curves across the Nith from the western slopes of Kirkpatrick Hill to Cleugh and the hillside above Newhall, and with a break from Brownhill to the east of Closeburn. Later mounds with outwash fans were mapped about Closeburn and between this village and Thornhill. Slightly younger moraines follow the western side of the valley from the south-west of Penpont, and on the eastern side discontinuously to Gatelawbridge and Morton Castle.

The glacier streaming along the Shinnel valley became detached and deposited the moraine skirting the hillside near Shinnel Bridge.

A magnificent series of moraines, contemporaneous with the above, is displayed along the banks of the Cairn Water.† They begin about 2 miles south of Dunscore. The outermost member can be traced from the valley of the Collieston Burn along the western side of the Cairns Water to Upper Stepford, along the flanks of the Cat's Craig to the hill-slopes north of Dunscore, by Bów, Kirkbride, and Fardingjames. Countless ridges and mounds, arranged on numerous lines concentric with this moraine and on its inner side, curve into the depression north of Dunscore. The overflow of the waters, impounded by the ice, drained by the large valley of the Glemmidge Burn into the Nith.

The ice which had overflowed the lower south-eastern slopes of Slatehouse Hill into the Glenesslin Burn gradually withdrew behind this ridge into the valley of the Cairn Water, where the crescentic ridges mark the step-wise retreat of the Cairn Water glacier in the direction of Moniaive.

(d) *The Kirkconnel Series.*—Sand and gravel moraines cover the broad floor of the Nith valley over the stretch between Sanquhar and Old Cumnock.‡ Below Sanquhar the crescentic and concentric ridges, curving along the hillside, are convex to the south, while between Old and New Cumnock they are convex to the north; the change in the direction of convexity appears to take place east of Kirkconnel. These moraines represent a retreat stage not only of the Nith Glacier, but also of the Lugar Water Glacier, which at earlier periods was confluent with the northern ice. The later part of this phase is, in general, but poorly represented. Usually it is restricted to a single moraine in each of the valleys, e.g. at Auchenstroan in the Craigdarroch valley, at Marwhirn in the Dalwhat Water, and at Craigercoon in the Shinnel Water. Occasionally it is quite absent, as in the Chanlock Burn, Kello Water, and Scar Water, though the mounds are numerous in Glenmanna, tributary to the latter. Only in the Euchar Water are the moraines finely displayed; here they extend from below Benzie Craig to above Buchan Head. This phase is also virtually wanting in the valleys tributary to the Nith from the Lowthers.

(e) *The Corrie Series.*—These corrie moraines were found in the Lowthers and in the hills north-west of Moniaive.

\* *Proc. Geol. Soc.*, iii (1840), p. 323.

† *Ibid.*, Sheet 14 (1869), p. 25.

‡ *Mem. Geol. Survey*, Sheet 9 (1877), p. 39.



### 5. *The Annandale Glacier.*

The Annandale Glacier was fed by ice from the Lowther Hills and from the mountains to the east. The country east of the Annan was not examined.

(a) *The Cummertree Series.*—This typical kettle-moraine, over 1 mile in width, begins as a definite feature about Dalton, trending slightly east of south as far as Cummertrees, whence it curves to the east by Newbie to Annan, Waterfoot, and the Solway. Occasional branches, possibly representing retreat stages, seem to swing out of this moraine about Kinmount House and south-east of Dalton.

(b) *The Lockerbie Series.*—Moraines were noticed north-west of Lockerbie and about 2 miles north-west of Lochmaben; the peculiar relief to the south of Lochmaben may also be, in part, morainic. To this stage would also seem to belong the esker ridges on either side of the dale, the one, relatively short, about 2 miles south of Lockerbie, the other, much larger, about 2 miles south of Lochmaben. No further moraines were noticed in Annandale, except the doubtful ones at Granton.

(c) *The Queensberry Series.*—A series of moraines were mapped in the valleys, draining eastward to Annandale, below Moffat. They occur in the Garpel Water, extending at intervals down the valley to within 1 mile of the Evan Water. This glacier formed a small lake just west of Beattock Hill, which discharged southward by a dry valley into the Kinnel Water. Equally well developed, though fewer in number, are the moraines in the valley tributary to the Evan Water at Middlegill, and those in the Threepen Burn and Lothan Burn, about Lothanhead and above this locality.

(d) *The Corrie Series.*—These are found in the Lowther Hills.

### 6. *The Upper Clydesdale Glacier.*

The Upper Clydesdale Glacier was nourished by the snows on the Lowther Hills and the Culter Fell Range; this range was not examined. South of the Carstairs moraine, Upper Clydesdale is poor in moraines, as R. CHAMBERS\* noticed.

(a) *The Elvanfoot Series.*—Apart from doubtful lateral moraines and other uncertain morainic features observed near Lamington, about Robertson, and in the Clyde valley south of its confluence with the Glengonnar Water, the first indisputable moraines were found near Elvanfoot; they occur on the hill-flank  $1\frac{1}{2}$  miles south-east of Newton and nearly 1 mile south-east of this place on the south-east slopes of Watchman Hill. Drainage channels connected with these glaciers were observed at Dunmoss, about 2 miles west of Elvanfoot and on the south-east end of Cruereoch Hill.

(b) *The Nether Fingland Series.*—Much later than these moraines are the mounds at Nether Fingland in the valley of the Patrail Water and the corresponding ones at Tiddle Moss in the valley of the Elvan Water.† Other moraines occur in the Daer Water, near its confluence with the Kirkhope Cleugh and also below, and doubtfully above, its confluence with the Carsehope Burn.

(c) *The Corrie Series.*—These moraines occur in the Lowthers and Leadhills.

### 7. *The Doon Glacier.*

In the track of the Doon Glacier moraines are very few and relatively insignificant.

(a) *The Clawfin Series.*—Moraines, about 1000 feet above the sea, run across the valley

\* *Ancient Sea Margins* (1848), p. 217.

† *Ibid.*, p. 218.



east of Dalmellington, between Benbreock and Clawfin.\* A small ridge occurs south of Straiton.

(b) *The Loch Doon Series*.—As Sir A. GEIKIE observed,† some of the islets of Loch Doon “look like tops of morainic mounds” and may represent the summits of a submerged series of moraines. Occasional moraines were mapped farther south, *e.g.* those running from the north-west foot of Hoodens Hill to the Eglin Lane and, much better displayed, those in the Gala Lane, extending to a distance of 2 or 3 miles from the Tauchers. Mr J. SMITH speaks of a moraine of angular blocks at the Ford of Moak, Loch Doon.‡

(c) *The Corrie Series*.—Corrie moraines occur in the Gala Lane and on the east of the Merrick.

#### 8. *The Stinchar Glacier.*

(a) *The Colmonell Series*.—Moraines have been observed at Colmonell where they span the valley. They can also be traced at intervals along the southern flanks of the valley, at a considerable altitude, to the east of this. In the Duisk they can be recognised curving from the hillsides into the central line of the valley, *e.g.* just below Barrhill, at Barbour, at Glenduisk, and near Pinwherry Station. North of Barrhill they were followed on the moors from west of Mill Loch by Rotten Loch to Shalloch Well. Later and lower ones sweep from White Fell plantation in the direction of Barbour, and from Leggan Loch by Barbour to below Barrhill. These were all formed by the ice which poured from the basin of the upper Cree into the Duisk valley. Moraines of the same age were observed north and south-west respectively of Pinmore Station, and near Mark in the valley of the Muck Water.

(b) *The Corrie Series*.—The corrie moraines of this glacier are those of the Cree Glacier.

#### 9. *The Corrie Moraines.*

The Corrie moraines are finely displayed in this part of the Southern Uplands. In the Merriks they are specially well developed; in the west, in the corries of Crossburn and Kirshinnoch Burn, north and south respectively of Kirriereoch Hill, and in those at the head of the Kirkennan and the Knocklach Burns; on the east, as small morainic mounds in the Caldron Burn, about and below its confluence with the Eglin Lane. Moraines also occur east of Loch Twachlan, under the eastern slopes of Kirriereoch Hill and in the upper parts of the Gloon and Buchan Burns.

West of the Gala Lane a fine series of corrie moraines was observed; the best were formed by the corrie glacier issuing from the Tauchers. They also occur west of the Round Loch of the Dungeon and the Long Loch of the Dungeon, laid down by ice from the depression south of Dungeon Hill. A series of moraines lies at the foot of Craginaw Hill.

In the Rhinns of Kells these features were noticed at the head of the Garryhorn and of the Polmaddy Burn around Elderholm; east of and around Loch Harrow, east of Loch Minnoch, and in the upper part of the Folk Burn. They are also well shown around Loch Dungeon, up the Hawes Burn toward Corserine, and in the corrie situated east of Meikle Millyea and drained by the Minnigall Lane.

In the Lamachan Hills the moraines lie in the corries east and west of White Hill, toward the head of the Penkill Burn and south of Cairngarroch.

In the Cairnsmore of Fleet a fine suite was noticed, especially in the corries on the eastern

\* *Mem. Geol. Survey*, Sheet 14 (1869), p. 25.

† *Scenery of Scotland*, 3rd ed. (1901), p. 350.

‡ *Brit. Assoc. Handbook, Glasgow* (1901), p. 523.

side, *e.g.* at the head of the Mid, Carrouch, and Cuthiemore Burns. They were also found, though smaller, in the corries west of Meikle Mulltaggart and south-west of Craignelder.

In the Cairnsmore of Carsphairn and adjacent hills a number were also mapped. They were formed sporadically on the western slopes of Cairnsmore of Carsphairn; in the Polwhat Burn, in the Poldores Burn, and at Beninner Gairy; in the Bow Burn and at Gairy of Cairnsmore; at the foot of the east and west slopes of Moorbrock Hill; in the Keoch Lane; in the Holm Burn, where they are most finely displayed,\* and can be traced as far south as Nether Holm of Dalquhairn; on the western flanks of Coranbae Hill; at Manwhill† and for about 1 mile below this place; in the corrie north of Meikle Dibbin Hill; above Shinnel-head; in the Snout and Lorg Burns, east of Polskeoch; doubtfully at the head of the Scar Water; in the Afton Water near Montraw and in the Montraw Burn; east of Struthers Brae and at intervals of about half a mile in the Craig Burn.

Small corrie moraines were found to be singularly scanty in the Lowther Hills. They were mapped among other places at the Dalveen Pass, in the Glen Franka Burn; in the Shortcleugh Water, near Windgate Foot, near the confluence of the streams north-east of Windy Knoll; in the Riccart and Lang Cleugh, south-east of Green Lowther and near the head of Lothan Burn. They were also observed in the valleys draining the southern slopes of Queensberry; in the Water of Ae near Craigshiels; in the Deer Burn and on the hillside where the Pishnack Burn enters the Ae. Later ones were found west of Muir Hill and on the flank of the Ae Valley between the tributaries of the Clerk Grain and Aen Grain.

In the Capel Burn, flowing from the western slopes of Queensberry, lateral moraines are well shown. The water issuing from this glacier was apparently impounded to form a lake south-west of the Law, by a glacier standing in the valley of the Garroch Water. This glacier produced marginal drainage channels and deposited coarse gravels with interbedded sands on the face of the hills east of Locherben,‡ north of Garroch at 1000 feet, and also north of Locherben and east of Mitchellsacks. It was very difficult to decide whether this was a local glacier or the edge of more powerful ice from the west.

A small corrie moraine was noticed at the north-east of Criffell. Earthy and gravelly deposits near the sources of the streams are possibly morainic.§ Moraines were found at the mouth of the Devil's Beef Tub in the Moffat Water.

#### IV. CORRELATIONS OF THE MORAINIC STAGES.

The moraines of the different glaciers have now been described; their distribution is brought out on the map. It is now proposed to discuss the correlation of the moraines of these widely separated regions, and so fix the limits of the glaciers at the various stages of recession. The criteria which have served as guides in this attempted correlation are considerations of relief, *i.e.* altitude and valley extent, the relative sizes of the glaciers measured in surface extent, the type of moraine, and the geographical position. The best method would doubtless be the determination of the altitude of the snow-line; but as the snow-line can only be worked out from the moraines, this method is obviously impracticable. Correlation, difficult under the best conditions, is rendered still more so by the incompleteness of the record; gaps, generally short but frequently of considerable length, interrupt, for reasons seldom determinable, the continuity of the moraines. Glaciers fed by the snows of the same

\* *Mem. Geol. Survey*, Sheet 15 (1871), p. 40. Here are described some of the other moraines noticed in this paragraph.

† *Ibid.*, Sheet 9 (1877), p. 39; others in this area are described on pp. 40, 41.

‡ *Ibid.*, p. 43; here regarded as raised beaches.

§ *Mem. Geol. Survey*, Sheet 5 (1896), p. 36.



hills, possessing the same aspect and flowing on parallel courses, have produced in the one case a magnificent series of morainic mounds and ridges strewn thickly over the sides and floor of the valley for a distance of several miles, while in the other valley there is a complete absence of moraines, though presumably the same periodic or unperiodic halts marked its recession. As instances of this striking contrast may be cited the valleys of the Euchar and Kello Waters, west of Sanquhar, and those of the Garpol and Kinnel Waters, west of Moffat.

Another cause of uncertainty is introduced by the closely related fact that a large and conspicuous moraine, to all appearance the product of a prolonged and important halt, may apparently elsewhere be represented by a ridge of very attenuated character and insignificant appearance. A further difficulty is caused by the occurrence, as in the case of the Cree and Ken Glaciers, of large glacial centres situated on their flanks.

The Cree Glacier has been chosen as a standard of comparison, as here the moraines are quite distinct, sharply defined, and well distanced, and the relief of the bed of the glacier relatively simple. In connection with this glacier, as already pointed out, there were observed five stages: (a) the Monreith Stage; (b) the Kirkcowan Stage; (c) the Newton-Stewart Stage; (d) the Minnoch Stage; (e) the Corrie Stage. The names of these stages will be used to cover all the corresponding moraines of the valley glaciers of this region.

#### (e) *The Corrie Stage.*

The corrie moraines of all these mountain centres may, with little apprehension, be regarded as of the same age, for, generally speaking, in those mountains which have the greatest elevation the corrie moraines attain their maximum development and horizontal and vertical distance from the corrie walls, while in the lower hills they extend to only a small distance. In almost all cases they are best displayed in the corries facing north or east, *e.g.* in the Merrick and Kells ranges, the Lamachan Hills, Cairnsmore of Fleet, Cairnsmore of Carsphairn, and the Lowther Hills. This is modified in certain cases, for example, in that part of the Merrick range south of Shalloch on Minnoch and about Kirriereoch where the moraines are well developed in the west, and but indifferently, if at all, in the east. This departure from the general rule is doubtless due to the relief; on the west, large valleys penetrate into the hills: on the east, these fall steeply as one face, more or less continuous and in general alignment. Similar relief conditions characterise the Kells range; here, however, the valleys face east and so have emphasised the normal tendency, bringing about the striking contrast presented by the magnificent corrie moraines of the east, *e.g.* the Dungeon moraines and the diminutive and scanty moraines of Elderholm in the west.

#### (d) *The Minnoch Stage.*

The greater the distance from the ice-centres, the less certain becomes the correlation, as the moraines of one or more stages may have been entirely suppressed or possibly later eroded by Late-glacial or Post-glacial streams. Yet with the Minnoch Stage of the Cree Glacier is obviously to be correlated the Carsphairn series of the Ken Glacier. In the Dee, this phase is but ill-developed, but is represented by the moraines extending into the head of Glen Trool and down the Dee to the east of Craigen callie. Its poor development is clearly due to the general absence of big corries in which the glaciers could be fed, which, as just observed, was responsible for the rarity and smallness of the corrie moraines of this region at a later stage. The same causes were operative in the Doon, though here Loch Doon

is an additional complication. To this stage doubtless belong the Kirkconnel series of the Nith Glacier, the Big Water of Fleet series of the Fleet Glacier, and the Nether Fingland series of the Upper Clydesdale Glacier.

(c) *The Newton-Stewart Stage.*

At this stage of the Cree Glacier the Merrick and Lamachan Glaciers were united in the valley of the Cree, the front of the confluent ice extending from Newton-Stewart to The Knowe. As can be readily gleaned from the map, an extension (in inverse order) of the Cree Glacier from the Minnoch stage to Newton-Stewart would carry the ice in the upper Cree down the Duisk as far as Colmonell; that the ice along the line of union was not thrust farther than The Knowe is due to the obstruction of Garwall Hill. These series may be safely correlated. With this stage it would also seem safe to link up the Gatehouse series of the Fleet Glacier and the Laurieston and Crossmichael series of the Ken Glacier and the Cairn Water and the Closeburn series of the Nith Glacier. The greater extent of the Ken Glacier as compared with that of the Cree is clearly due to the nourishment of the first by glaciers from both east and west, while the Cree Glacier, in virtue of the relief, was fed only from the east. In Annandale no moraines of this age appear to be developed unless some of the sand and gravel accumulations near Moffat, interpreted as river and outwash terraces, should prove to be morainic. This stage would seem to be represented in Upper Clydesdale by the Elvanfoot series. In the Doon it is apparently absent (see below).

(b) *The Kirkcowan Stage.*

The Cree and Dee Glaciers were at this stage confluent and spread out as a Piedmont Glacier over the floor of Wigtown Bay. The Ken Glacier extended to the Southwick and Twynholm moraines, the Nith Glacier to the Dumfries moraines, and the Annandale Glacier to those of Lockerbie.

Along the north from Upper Clydesdale to the Stinchar at Ballantrae, the ice from the Southern Uplands was united with that from the Highlands and from Arran. Hence along this belt of country moraines of this date are wanting. The same explanation would seem to account for the absence of moraines of the Newton-Stewart stage in the Doon, as already noticed, and in the area of the Lugar Water.

(a) *The Monreith Stage.*

This stage, which was represented in the area of the Cree Glacier by a series of small moraines, is apparently developed, except in Nithsdale and Annandale, nowhere else in this region; on the north all the glaciers were united with the Highland ice; on the south they deployed over the area now covered by the waters of the Solway Firth.

The greater dimensions of the Kirkbean and Cummertrees moraines of the Nith and Annan Glaciers respectively, compared with the corresponding moraines of the type glacier, suggests that in this area only the later parts of this moraine are now to be found, and that the Cree Glacier extended during the earlier parts of this period of halt out on to the floor of the present Luce Bay.



## V. READVANCE MORAINES.

In the foregoing description it has been tacitly assumed that the moraines represent merely pauses in the general recession. For reasons which it is now necessary to consider, some of the stages, possibly all, would appear to mark the limits of readvance of the ice of considerable importance and magnitude.

The clearest evidence for such a readvance is connected with the Kirkcowan stage, particularly in the region of the Cree Glacier. Here, as an inspection of the map will show, the drumlins west of Wigtown Bay exhibit a striking discordance of trend, being divisible into two quite distinct systems, the drumlins of the one set running steadily north-east south-west, or approximately so, those of the other, equally uniformly north-north-west south-south-east, or almost at right angles to the drumlins of the first set. These extend from a line trending roughly from Kirkcowan to Garliestown westward over the whole of the Machers to the eastern shores of Luce Bay. The second set is confined to the east of this tract.\* If the distribution of these features be still more closely examined, it will be found that the two sets are mutually exclusive and that the line of delimitation is accurately coincident with the line of the outermost moraine of the Kirkcowan stage where this has been detected. It is clearly possible to insert lines across the gap between the stretches of moraine and coincident with this line of demarcation of the divergent drumlin trends which shall faithfully represent the edge of the ice in these places at the time when the outermost moraine of the Kirkcowan stage was being laid down. This shows, for example, the edge of the ice to have lain roughly along the course of the river Bladnoch, between Bladnoch itself and Kirkcowan.

These two series of drumlins, the one within, the other without the moraine, demonstrate different directions of ice-flow over the two regions. It might be assumed that these two series were produced simultaneously, the one by ice flowing along the valley of the Cree, the other by ice flowing at a slightly higher level across the Machers. But the line of demarcation is so sharp, the valley of the Cree so broad, and its western slopes so gentle, that such an application of the "deflection principle" of LOUIS AGASSIZ and J. GEIKIE is clearly untenable. The complete absence of drumlins exhibiting intermediate trends militates equally clearly against the view of the successive formation of the features as the Cree Glacier gradually fell back into the valley of the Cree. It seems necessary, therefore, to conclude that the drumlins within and without the moraine are the products of two distinct "glaciations" separated by a retreat of uncertain magnitude. The drumlins are regarded as sub-glacial or englacial features.

The corrie moraines are probably likewise due to a readvance. The writer's attention was first directed to this important question by Dr J. HORNE, who had recognised its significance during his official survey of the area. This readvance can only be detected where the direction of the ice-flow during the corrie phase differed from that of the preceding stage, causing the corrie moraines to have a different composition from the other moraines of the same area. This is probably best shown in the valley which falls northward, just south of Loch Dee. The preceding glaciation was from the north, up the valley, and transported granitic material from Loch Dee on to the lower Palaeozoic rocks. The later glacier was charged with this local material and flowed northward down the valley.

Two of the five stages would appear, therefore, to mark the limits of readvances. It seems probable that the others are likewise associated with readvances, and that more

\* In consonance with this newer series of drumlins is the striated surface observed just east of Grange of Bladnoch.

detailed examination may demonstrate such a connection. These oscillations are difficult to prove and can, in general, only be detected where for any reason the direction of ice-flow was changed. This may be conclusively proved for only a small part of the ice-front at any one stage, but if the correlation be correct, may with safety be extended to the other moraines of the same age.

## VI. SOME GENERAL CONSIDERATIONS.

### (a) *The Late Glacial Sea-level.*

The raised beaches of this coast have been frequently described. The 25-foot beach, usually at a somewhat lower level than this figure, is generally and widely developed along the coast. Higher beaches have been often noticed, *e.g.* the 40-foot beach at Lendalfoot, Ballantrae, the mouth of the Stinchar,\* and north of Girvan;† the 50-foot beach at Ballantrae,‡ between Ballantrae and Bennane Head,§ at Maxwelltown,|| at New and Old Abbey, Mainsriddle, Kirkcudbright, and Gatehouse;¶ the 60-foot beach at Kilwinning,\*\* and beaches at 60–75 feet in the Rhinns of Galloway,†† and at Ballantrae.‡‡

Though these were not made the subject of special study during this research, the occurrence and distribution were carefully noted because of the light they throw upon the Late- and Post-glacial sea-levels and their association and relation with the glacial deposits.

The occurrence of beaches at altitudes of approximately 25, 40–50, and 60 feet is indisputable. The existence of higher beaches is less certain and more difficult to establish on account of the erosion accompanying the later beach formation, and the internal and external similarity of the beaches to the contemporaneously formed fluvio-glacial deposits. Outwash fans and plains were found associated with all the major glaciers, *e.g.* in the Cree, Dee, Nith, and Annan valleys, and in those of the north. In the past these deposits have been frequently mistaken for raised beaches. Though their separation is by no means easy, in most cases it may be accomplished without too great difficulty. A fluvio-glacial, rather than a marine origin, is suggested by the fact that the accumulations proceed from the outer edges of the larger moraines, that they occur frequently at altitudes which have not in recent years been generally accepted as the height of the Late-glacial seas of Britain, *e.g.* at 200 or 250 feet above present sea-level; that they have a perceptible, though sometimes only slight fall seawards; that they possess a strong current bedding down the valley and are devoid of sea-shells.

Where, as usually happens, the undoubted outwash plains grade into equally indisputable sea-beaches, characteristically exhibiting sloping upper surfaces, it was found almost impossible to ascertain the height of the sea into which the fluvio-glacial streams were discharging their sediments for the building-up of the beaches. It is this difficulty which has introduced the uncertainty into the determination of the highest Late-glacial sea-level in this region. In the majority of places, if not in all, this would seem to have lain between 60 and 80 feet above present sea-level, though, as in the vicinity of Glen Luce and in a few places in the Rhinns of Galloway, there are indications of a 100-foot beach. Farther eastward no trace of this higher beach was discovered.

\* J. SMITH, *Trans. Geol. Soc. Glasgow*, xi, Suppl. (1898), p. 14.

† *Mem. Geol. Survey*, Sheet 7 (1869), p. 15.

‡ J. W. GREGORY, *Scot. Geogr. Mag.*, xxv (1909), p. 315.

¶ *Ibid.*, Sheet 5 (1896), p. 37.

†† *Mem. Geol. Survey*, Sheet 1 (1872), p. 9.

‡ *Ibid.*

|| *Mem. Geol. Survey*, Sheet 9 (1877), p. 43.

\*\* J. SMITH, *op. cit.*, p. 14.

‡‡ *Ibid.*, Sheet 7 (1869), p. 15.



(b) *The Origin of the Corries and U-valleys.*

The coastal peneplain of Ayrshire, Kirkcudbrightshire, and Wigtownshire rises inland to form the broad, flat-floored pass of the Nith, over the stretch from Sanquhar to Old Cumnock, at a height of about 700 feet above sea-level, of Carsphairn at an altitude of 600 feet, and of the Doon and Dee, between the ranges of the Merrick and Kells, at a height of 700-900 feet.

The rejuvenated gorges dissecting this peneplain are found in the Nith between Sanquhar and Thornhill, in the Lugar Water about Old Cumnock, in the Clyde about Lanark, in the Deugh at the Tinkler's Loup, in the Dee below Loch Dee, in the Water of Trool above Loch Trool, in the Duisk below Barrhill. The gorge of the Ness Glen at the north end of Loch Doon and the similar feature at the south end of Loch Grennoch may be partly of sub-glacial origin.\*

This peneplain rises into the hills and is continuous with the floors of the lower corries. These in turn dissect an older peneplain of a much higher level, of which remnants only remain, which carries the higher cirques, as displayed in the Lowther Hills.

As observed in the north-west of Ireland, the corries are but the modified heads of rejuvenated valleys cut into the higher peneplains, while the U-valleys represent the widened and steepened rejuvenated gorges dissecting in general the intermediate peneplain and opening on to the lower one bordering the coastal plain.

The larger lakes, *e.g.* the Lochs Doon, Dee, Trool, and Ken, mark the sites of the rock basins excavated by the ice in the lowest peneplain.

(c) *The Altitude of the Glacial Snow-line.*

By the application of the Partsch and other methods for the determination of glacial snow-lines, the following approximate values for the climatic snow-line in this part of the Southern Uplands were obtained; for the Kirkcowan Stage, about 900-1000 feet above the present sea-level, for the Newton-Stewart Stage, about 1200 feet, and for the Corrie Stage, about 1500 feet.

## VII. SUMMARY OF CONCLUSIONS.

The Southern Uplands, west of Annandale and Upper Clydesdale, were glaciated in the main by local ice centred in the hills extending from the Merrick, Corserine (in the Rhinns of Kells), Cairnsmore of Carsphairn, and the Lowther Hills. From this axis the ice radiated outward, to the south along the Cree, Ken, Nith, and Annan, to the north along the Upper Clyde, the Lugar, and the Doon, and to the south-west by the Stinchar and Girvan. The glaciers flowing to the north-west were deflected by the northern ice in the Firth of Clyde through west into south-west, and caused to pass over the Rhinns of Galloway. The glaciers issuing southward from the axis were compelled by the great press of ice in the Solway Firth, to which they themselves in large measure contributed, to flow south-westward over the Machers of Wigtownshire, and eastward from Criffell along the northern shores of the Solway Firth.

During the retreat the local ice split up into a series of more or less independent glaciers in occupation of the major valleys mentioned above. Their stages of recession are

\* Sir A. GEIKIE, *Scenery of Scotland*, 3rd ed. (1901), p. 348.

indicated by well-marked moraines (see map). In the valley of the Cree these fall readily into five distinct stages, which, proceeding in the order of formation, were denoted as the (a) Monreith, (b) Kirkcowan, (c) Newton-Stewart, (d) Minnoch, (e) Corrie Stages, each named after the locality where its best development is to be found. These stages were discovered in the valleys of the other glaciers and have been correlated with those of the type glacier in occupation of the valley of the Cree.

The absence of some of the outer moraines in the regions of the northern glaciers, from the Clyde to the Stinchar, is ascribed to the confluence of these glaciers at these earlier stages with the Highland ice. The partial development of the outer moraines in the Solway area indicates in a similar manner the union of the adjacent glaciers to form a broad Piedmont fan spread over the floor of the Solway Firth.

The moraines of the Kirkcowan Stage are shown by the discordance of the drumlin trends to mark a re-advance of the local ice of uncertain but possibly considerable magnitude. The corrie moraines likewise denote a re-advance.

In this region the Late-glacial sea-beaches seem to be definitely traceable to a height of 60–80 feet above the present sea-level, less certainly in isolated instances to 100 feet. The higher beaches grade imperceptibly into the fluvio-glacial outwash fans of the valley.

Corries and U-valleys are regarded as rejuvenated features glacially modified.

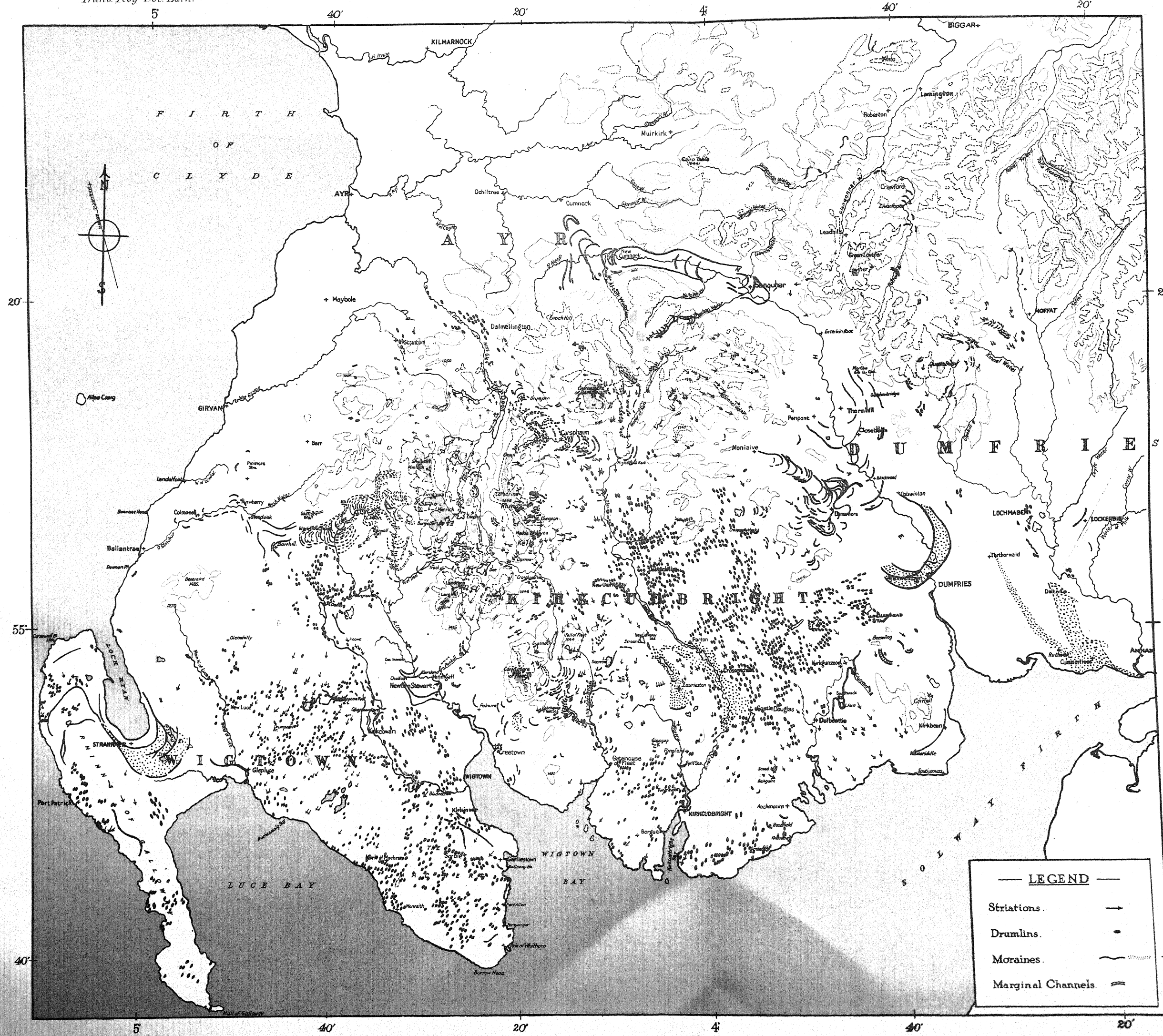
Approximate values for the glacial climatic snow-line of this area were ascertained; for the Kirkcowan Stage a figure of 900–1000 feet above the present sea-level was obtained, for the Newton-Stewart Stage of 1200 feet, for the Corrie Stage one of about 1500 feet.

#### EXPLANATION OF MAP.

Map showing by striæ and drumlin symbols the trend of the ice over the Southern Uplands, west of Annandale and Upper Clydesdale, and by morainic symbols the mode of retreat of the ice, of which five stages are recognised.

Relief Tints.—Uncoloured = below 1000 feet; light brown = 1000–1500 feet; dark brown = 1500–2000 feet; green = above 2000 feet. Scale: 1 inch =  $6\frac{1}{2}$  miles, approximately.









II.—The Readvance, Marginal Kame-moraine of the South of Scotland, and some Later Stages of Retreat. By J. Kaye Charlesworth, D.Sc., Ph.D., F.G.S., Professor of Geology, Queen's University, Belfast. *Communicated by Dr J. HORNE, F.R.S.* With 1 Map (Black and White).

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I. INTRODUCTION.

In the course of researches into the glaciation of the western part of the Southern Uplands of Scotland the writer accidentally stumbled upon a series of large and continuous moraines bordering the Central Valley. Some of these had been observed and described by earlier workers, others—probably constituting the larger part—had either escaped detection or had been differently interpreted.

The solution of the problem presented by these moraines not only required their careful mapping from coast to coast, but also inevitably led to an attempt to decipher the history of the retreat of the ice out of the Central Valley.

The results of these investigations are embodied in this paper. Throughout the discussion, and as far as my reading extends, reference has been made to the earlier literature and to the evidence of earlier workers. This not only makes it possible to dispense with detailed descriptions of the individual accumulations and the related phenomena, but also, in general, tends to the confirmation and strengthening of the views and conclusions to which the study of the area has finally led me.

II. THE GENERAL CHARACTER OF THE KAME-MORAINES.

The great morainic belts which are the subject of this communication are, without doubt, the most conspicuous and easily recognisable and determinable of the drift formations. Over much of their extent they present the appearance of a rolling belt of country in which countless hillocks and hollows, ridges and troughs, succeed each other rapidly and tumultuously.

They exhibit the bold, billowy relief of the swell and sag topography, with rapidly shifting curves and knobby and choppy surface, or a more subdued relief and gently undulating scenery. In general, they are kettle-moraines, pitted with numerous kettle-holes of varying depth and size, marked by small lakes, marshes, bogs, or meadows. These features show a marked tendency to parallelism with the course of the moraine. Channels formed by running water are also frequently clearly recognisable.

In their constitution the moraines are very variable. Boulder-clay, sand, and gravel are found frequently in intimate association or are developed in separate areas. Generally, they consist of water-worn sands and gravels, the coarser and finer material preponderating in different places. They show a special tendency to stratification where considerable drainage was associated with their formation, as where they crossed valleys and depressions. The surface is usually rougher where gravel is the chief constituent, and more softened where boulder-clay preponderates. Where the moraines consist of sand, they can be recognised by the lighter green of the vegetation in addition to the characteristic dimples in the surface. Boulders are often dotted over them.

When compact or loose boulder-clay occurs, it may be only superficial or penetrate to considerable depths, or even to the base of the deposit. These boulder-clay areas often show the characteristic morainic topography; there are, indeed, all gradations from the kame-moraines of sand and gravel to the country with kame form, but lacking the kame structure.

As the moraines usually skirt the hillsides they are but rarely associated with considerable outwash fans; gravel trains were observed, however, in the larger valleys leading from them. True eskers, *i.e.* accumulations clearly referable to the mouths or the channels of subglacial streams, were occasionally noticed, *e.g.* at Linnhead, south of Lanark. These features, however, are exceptional.

The moraine partakes of the nature of true moraine, kame- or kettle-moraine, overwash and outwash fans, lake deltas and floor deposits. Streams descended the ice-margin, subglacial rivers formed eskers at their place of emergence or possibly within their walls, debris rolled down or was shot over the face of the ice, while further confusion was added by subsequent stream erosion and deposition, by the overriding of earlier deposits during temporary readvances or oscillations, with the resultant erosion, disturbance, stau-effects, the intercrossing of single ridges, and the covering of earlier morainic ridges by later outwash materials.

Such oscillations within the belt are shown by the overriding of outwash or overwash sand and gravel or lake clay and sand, with the consequent intercalation of these in the boulder-clays. Though caution needs to be exercised in interpreting such intercalations, as these do not necessarily imply oscillations, in this region these structures seem to be of this origin. Such intercalations were noted by Professor P. F. KENDALL and Mr E. B. BAILEY \* on the northern slopes of the Lammermuir Hills. They are, however, common in other places, *e.g.* at Newmills, Galston, in the Gass, Guelt, and Glenmuir valleys, and near Dunbar. Such oscillations are further proved by the dissection by marginal streams of earlier deposits, by the deepening of previously abandoned marginal channels, by the choking of these valleys at their mouths by moraines, or even their entire obliteration by subsequent infilling.† Some of these cases may, however, be interstadial.

Complication of the deposits is further introduced by slumping, due to the gradual melting of derelict masses of ice, by settling consequent upon the melting of interstitial ice by underground drainage, and by consolidation.

\* *Trans. Roy. Soc. Edin.* (1908), xlv, p. 17.

† "Geology of East Lothian," *Mem. Geol. Survey* (1910), p. 175.



Drainage from the ice-free area contributed its quota of material, which was frequently very large, as has been shown by Professor KENDALL and Mr BAILEY,\* and added its own erosion effects. With a slight retreat of the ice-edge, dissection of earlier deposits by marginally directed streams took place, with the production of residual kamiform ridges and mounds, and the redeposition of the material as deltas or alluvial fans.

The moraine is the result of vigorous drainage from a wasting ice-sheet, yet one of sufficient thickness and vigour of motion to enable the rapid and heavy loss to be replenished.

In fine, these great kame-moraines may be expected to be composed of many genetically different formations, occasionally decipherable, usually and for the most part hopelessly inextricable. In their composition, variety of form, their topography and topographical relations these great accumulations, bounding the Central Valley on the south and festooned over it to the north, may be regarded as true moraines, in width, length, and form, as characteristic and as important as the great kettle-moraines of earlier glaciations, *e.g.* as that bounding the Newer Drift in North-west Europe, Switzerland, or North America.

Comprehensively they may be termed kame- or kettle-moraine, as they were formed marginally to the ice and were strictly controlled by it, and, speaking broadly, mark the line of the ice-margin at definite and important stages in the glaciation.

### III. "LAMMERMUIR-STRANRAER MORaine" AND THE MODE OF RETREAT.

The outermost morainic belt described in this paper skirts the northern flanks of the Southern Uplands, extending, without a break, from the east coast south of St Abb's Head to the Clyde above Lanark and the vicinity of New Cumnock, occurring again at Stranraer and in the Rhinns of Galloway. The ice-sheet at this stage was still extremely powerful; it overrode the Pentland Hills, abutted against the slopes of the Southern Uplands to an altitude exceeding in places 1000 feet, filled the shallow seas on the west, and spread far out over the sea-floor on the east.

It is now proposed to describe the course of this moraine—the "Lammermuir-Stranraer Moraine"—and the subsequent retreat of the ice-edge. The description will treat successively of certain large regions, working from east to west.

#### 1. *The Kame-moraine along the Northern Flanks of the Moorfoot and Lammermuir Hills.*

From Eddleston, about five miles north of Peebles, to the coast of the North Sea, south of St Abb's Head, there extends along the northern flanks of the Moorfoot and Lammermuir Hills, and at an altitude ranging up to 1100 feet above sea-level, a series of moraines of gigantic proportion. They are well displayed at Eddleston,† and run by Portmore Loch and Gladhouse Reservoir, south of Middleton House, on to the northern slopes of Falla, below Lammer Loch, by the Witches Knowe, across Hopes Water, by White Castle, Deuchrie Dod, south of Woodhall, north of Cocklaw Hall to Meikle Black Law, and inland from the cliffs to St Abb's Head, Eyemouth, and Lamberton. Their fluvio-glacial origin was noted by J. GEIKIE.‡

Throughout its length the ice-margin was maintained at approximately the same altitude, namely, about 900 to 1000 feet above sea-level; the greater distance from the source

\* *Op. cit.*, p. 14.

† *Ibid.*, p. 211.

‡ Cf. J. GEIKIE, *Great Ice Age*, 3rd ed. (1894), p. 17.

of the ice of the Lammermuir Hills as compared with the Moorfoot Hills, which might have been expected to have caused a diminution of thickness, was apparently fully compensated for by the freedom from the obstruction of the Pentland Hills and the ease of flow along the great valley and estuary of the Forth. Only toward the extreme eastern end did the ice-margin decline notably in altitude, owing to the rapid curving, to the south-east of Dunbar, of the hills which, further westward, had hemmed in the ice, and to the fanning of the ice-masses over the floor of the North Sea.

The drainage from the melting ice-sheet, reinforced by land drainage and probably by melt-waters from local glaciers in the Lammermuirs,\* was carried by the direct overflow valley at Heriot (intake, 884 feet O.D.)† into the Gala Lane, and by a series of marginal channels,‡ falling, in general, eastward along the flanks of the hills, discharging finally by Grant's House and the Eye Water.

More important are the moraines occupying the strip of country, occasionally a few miles wide, which lies to the north of this line of maximum readvance. This kettle-moraine extends along the north of the Lammermuirs from the south of Borthwick, by Costerton, east of Gifford and of Garvald, by Pressmannen Loch and Woodhall, and east of Cocklaw to Cockburnspath. It was described by Professor KENDALL and Mr BAILEY,§ together with the related marginal drainage features.

The large kame-moraine which runs along the Highland border to the south-west of Stonehaven, which Dr R. CAMPBELL kindly described to me, together with the associated marginal drainage channels,|| may tentatively be regarded as marking the northern edge of this ice at the period when it abutted against the Lammermuir Hills and fanned out over the North Sea. The front of the Dee Glacier lay at the same time off the coast to the east of Aberdeen.¶

## 2. Retreat of the "Esk Lobe" and of the Northern Ice in East Lothian.

The ice-sheet whose edge is delineated by these morainic and marginal drainage features filled the Central Valley, overrode the Pentland Hills, rested its flanks on the northern slopes of the Moorfoot and Lammermuir Hills, and was spread out to an indeterminate distance over the floor of the North Sea. When climatic factors caused a withdrawal of the ice-sheet, the shrinkage took the form of a falling back of the southernmost edge of the ice and a simultaneous lowering of its surface. The highest summits of the Pentland Hills, probably snow- or ice-clad, began in consequence to project as nunataks, their size, with progressive thinning of the ice, gradually increasing and causing a shadow area of low ice-pressure, finally an entirely ice-free zone, to arise in their lee, namely, about Penicuik. That this initial ice-free area in the corridor south of the Pentland Hills should be situated so far to the east is not surprising when it is borne in mind that the direction of ice-thrust was, in the main, from the west.

The earlier limits of this ice-free zone are indicated by the moraines about Penicuik. These appear to be of double origin, as from the above would seem probable, for they were formed along the edge of two ice-lobes, withdrawing to the north-east and south-west respectively out of the corridor.

The drainage from the melting ice-lobes escaped southward into the Eddleston valley; the height of the intake is about 900 feet O.D.

The mode of retreat of the eastern or "Esk Lobe" may now be traced. The direction of

\* P. F. KENDALL and E. B. BAILEY, *op. cit.*, p. 20.

|| A. BREMNER, *Trans. Edin. Geol. Soc.*, xi (1920), p. 34.

† *Ibid.*, p. 23.

‡ *Ibid.*, p. 20.

¶ *Ibid.*, p. 3.

§ *Ibid.*, pp. 13-20.



thrust of the ice was, generally speaking, from the north and north-east, around and over the north-east end of the Pentland Hills. The eastern part of the Penicuik moraine,\* in places 2 miles wide, swings across the corridor by Rosebery Reservoir to the south of Temple and Borthwick. The ice further east, in East Lothian, had likewise been falling back, and had reached the line of the Spott Burn and Eweford. The sands and gravels of the coastal strip south of Dunbar were formed successively,† partly as deltaic deposits, partly as true moraines, during this withdrawal.

A slight retreat within the Penicuik moraine made escape by the Eddleston valley no longer possible. It caused the initiation, by the impounded normal drainage of the River Esk and the melt-waters from the ice-edge, of the dry valley, intaking at approximately 800 feet O.D., which falls eastward to the Rosebery Reservoir, and by that running eastward from this reservoir, near Yorkston. This water escaped into the channel now occupied by the Middleton North Burn and so into the valley near Costerton. The floor of the Middleton North Burn lay at this stage at a considerably higher level. A slight recession in the Borthwick area, indicated by the large moraine running along the south-east slopes of Roman Camp Ridge, made possible the escape of the drainage by the Crichton Castle overflow, the water then flowing south of Pathhead; the corresponding ice-front continued over Haddington to the northern slopes of Traprain Law and Dunbar, as is shown by the sands and gravels strewn along this line.

The "Esk Lobe" then withdrew to the line of the big moraine, which curves from the eastern end of the Pentland Hills, over Roslin, Carrington, and Arniston Castle. During this retreat the waters impounded in the Midlothian Basin, forming "Lake Esk," excavated the channel which lies  $2\frac{1}{2}$  miles east of Penicuik. The surplus waters of this constantly enlarging lake were carried by the large valley, intaking below 600 feet, which runs from near Rosslynlee Station‡ to Stonefield, and by that skirting the eastern side of the grounds of Arniston Castle, escaping finally into the Crichton overflow.

The Roslin-Carrington moraine continues by the western and northern flank of Roman Camp Ridge to near Ormiston, the edge of the ice extending to the north-west of Garleton Hill. The drainage from "Lake Esk" escaped at this stage by the Crichton overflow into the Tyne Water. The dry valleys noticed by Mr G. BARROW, along the northern slopes of the Garleton Hills§ and near East Linton, doubtless mark a slightly earlier phase than that represented by this line, while those north of the hill of Balgone|| indicate a slightly later one.

A later moraine line traverses the Esk valley from near Loanhead, by Dalhousie Castle, Newton Grange, Whitewell, Cousland, Elphinstone, to the east of Tranent. The sands and gravels south of the Braid Hills are only in part morainic; they include the deltas of the streams flowing through the marginal channels south of these hills.

The next retreat stage is marked by the Dalkeith,¶ Carberry, and Tranent moraine, when the drainage escaped by the valleys south and east respectively of Crossgate Hall. The lower one intakes at about 330 feet.

The last phase of "Lake Esk" is given by the valley about half a mile south of

\* *Mem. Geol. Survey*, Sheet 32 (Edinburgh), 1910, p. 331.

† P. F. KENDALL and E. B. BAILLY, *op. cit.*, p. 16.

‡ The overflow channels at Carrington, Rosslynlee Station, and Rosewell were noted by J. COSSAR (*Scot. Geog. Mag.*, xxvii (1911), pp. 597, 598).

§ "Geology of East Lothian," *Mem. Geol. Survey*, Sheet 33 (1910), p. 179.

|| *Ibid.*, p. 180.

¶ "The Geology of the Neighbourhood of Edinburgh," *Mem. Geol. Survey*, 2nd ed. (1910), p. 331.

Prestonpans which cuts the 150 contour.\* With the abandonment of this outlet the lake ceased to exist.

During the whole of the recession of the "Esk Lobe," traceable by moraines and marginal channels, the Midlothian drainage had to pass right across East Lothian to reach the sea.†

Meanwhile the Northern Ice was falling away from the northern slopes of the Pentland Hills. One phase is marked by the sands and gravels covering the floor of the hollow west of Bavelaw Castle at a time when the melt-waters flowed over the col into the Loganlee valley,‡ and at a slightly later stage by the col leading into the Glencorse valley.§ These streams deposited deltas in "Lake Esk," apparently at the stage of the Roslin-Carrington moraine.

It may here be stated that the sands and gravels at and slightly below the 100-foot contour near Dunbar are here regarded as true morainic materials, and not as part of the 100-foot beach. This interpretation is confirmatory of the view expressed by Professor P. F. KENDALL and Mr E. B. BAILEY with regard to the altitude of the late-glacial sea-level in this area, based on the height of the mouths of certain overflow channels.||

### 3. *The Southernmost Kame-moraines from Eddleston to Biggar.*

The southernmost kame-moraines, which rise so conspicuously along the whole length of the Moorfoot Hills, continue in a roughly south-westerly direction from Eddleston at an altitude of about 1000 feet, swinging round the shoulders of the hills south of Lamancha Station and following the hillside at about the same elevation. They extend into the recesses, as south of the Kaimies and along the Tarth Water, south-east of Blyth Bridge, continuing westward beyond Harestanes and Lochurd to the Mount, about one and a half miles north of Kaimrig End, ending here quite clearly and sharply in the valley west of Lochurd Hills (1632). From here the moraine is continued round the hillsides toward Melbourne, along the western flanks of Broomy Law, east of Brownsbank, and round hill 1127 towards Kaimrig End, whence it follows the stream flowing south to the Biggar Water. It skirts the hillside about one mile east of Skirling, continuing east of Skirling Mains across the Biggar Water on to the northern slopes of the hills south of Biggar and in the direction of Culter, where it appears to cease.

The drainage from the ice-edge escaped directly into the Biggar Water, also southward into this stream from Kaimrig End and Broughton and by the valleys of the Tarth and Lyne Water.

### 4. *Recession of the "Dolphinton Lobe."*

The ice in the lee of the Pentland Hills cleaved about Penicuik to form two lobes. The recession of the eastern or "Esk Lobe" has been sketched. An outline of that of the western or "Dolphinton Lobe" may now be given.

The Penicuik moraine, which skirts the flanks of the Pentland Hills, east of Walstone, curves under the grounds of Penicuik House to Leadburn and the hillside near Lamancha Station. The crescentic moraine, swinging from the southern slopes of the Pentland Hills to the south-east of Carlops, by Harlaw Main to Lamancha Station and Holmyre House, marks a later halt. The Auchencorth Moss is held up between these moraines. Later ones run from West Linton, across the Cairn Burn toward New Kaimhouse, where they join similar features which sweep

\* P. F. KENDALL and E. B. BAILEY, *op. cit.*, p. 31.

† B. N. PEACH in R. COCHRANE, *Pentland Walks* (1910), p. 146.

‡ *Op. cit.*, p. 31; "Geology of East Lothian," *Mem. Geol. Survey*, Sheet 33 (1910), p. 177.

§ *Ibid.*, p. 12.

§ *Ibid.*, p. 147.



from Mountain Cross by Kaims, Paulswell, under Broomlee, to the south of West Linton and on to the southern slopes of Mendick Hill.\*

In agreement with these are the marginal channels which occur on the southern flanks of the Pentland Hills and fall north-easterly, *e.g.* Windy Ghoul,† falling to Carlops, the one east of Stoneypath, that north of Carlops,‡ and the earlier one along the burn at Walstone, north of the moraine.

A later position is indicated by the moraine which curves from the side of Mendick Hill by Hyndfordwell on to the western flanks of Blyth Muir.

Until escape by the Lyne Water became possible, the lake about West Linton drained into "Lake Esk" by the Harlawmuir Burn, intaking below 900 feet.

The ice which flowed round Black Mount (1689) cleaved to the lee of this nunatak, *i.e.* to the south-east, about Melbourne. The eastern branch withdrew toward Dolphinton, depositing recession moraines, *e.g.* about Bank and Townhead, and on the eastern slopes of Black Mount. A later pause is indicated by the moraine running from the eastern flank of White Hill, under Dolphinton, east and north of Loanhead, by Garvald House toward Kirkland. A still later one is marked by the moraine spanning the valley west of Loanhead, from White Hill to Garvald House.

The western branch, formed by the cleavage of the ice, retreated in the direction of Elsrickle and laid down the moraines which sweep along the flanks of Black Mount to Melbourne and Broomy Law. The ice about Kaimrig End withdrew through the gap between hills 1127 and 1163, the ice about Skirling through the gap between hills 1163 and 936, falling back on to the line indicated by the moraines skirting the Biggar-Dolphinton road.

The Northern Ice parted from the Upper Clydesdale Glacier in the valley of the Biggar Water, and, retreating northward, formed the moraines on the hillsides bounding the gap north of Biggar.

The ice-edge during this phase is marked by the moraines running round the South Medwin valley, east of Dunsyre, by Walston, Howburn, Edmonston, and along the hillside east of Cocklaw, by Carwood, Huntfield, to Quothquan. The melt-waters from the ice at Carwood eroded the upper part of the channel falling southward to Biggar, while considerable drainage escaped, both at this and at a slightly later stage, eastward into the valley at Dolphinton.

During this period the Upper Clydesdale Glacier, parting from the Northern Ice about Skirling, withdrew westward along the Biggar Water to Biggar, where it also lost contact with the Northern Ice retreating toward Carwood, as noted above.

Simultaneously, the Northern Ice was gradually withdrawing from the western and northern slopes of the Pentland Hills; the distribution of its moraines will be sketched below (p. 34).

##### 5. *Retreat from the Region south of Carstairs.*

At the period of maximum readvance the Upper Clydesdale Glacier was confluent with the Northern Ice and this with the glacier descending the north slopes of Tinto. The moraines near the Carmich Burn and north-west of the Tinto Hills probably mark the edge of the Tinto Glacier during this phase.

\* The hummocky and conical mounds on the hill slopes between Linton and Dolphinton were early noticed (*Mem. Geol. Survey*, Sheet 24 (1869), p. 21).

† T. C. DAY, *Trans. Geol. Soc. Edin.*, xi (1924), p. 266.

‡ B. N. PEACH, *op. cit.*, p. 148; R. CAMPBELL, *Proc. Geol. Assoc.*, xxv (1914), p. 24.

There occur about Thankerton and near Symington two ridges of sand and gravel which have been frequently described and just as variously interpreted. They have been regarded as eskers formed by the Upper Clydesdale Glacier and as moraines of the same, and again of the Tinto Glacier. The writer's own reading of the field evidence is opposed to each and all of these views.

The discordance of views which has hitherto prevailed has been due to the difficulty of assigning to each of these glaciers—the one issuing from Tinto, the other from Upper Clydesdale—their respective rôles. It seems necessary, unfortunately, to add still further to the confusion by adding a third element—the Northern Ice—whose presence in the area has, apparently, up to the present been entirely unsuspected.

This region was, it would seem, the scene of the separation of the three elements—the Northern Ice, the Upper Clydesdale Glacier, and the Tinto Glacier.

The Thankerton ridge, which crosses the Clyde valley from the eastern foot of Tinto, appears from its position to be a moraine. It is difficult to picture a glacial stream from the margin of any of the three ice-masses which could form an esker, *in sensu stricto*, in this position. As a moraine its position is difficult to reconcile with the Tinto Glacier, as Professor GREGORY has done,\* and still more difficult with the Upper Clydesdale Glacier. Its continuation on to the north-west flank of Quothquan Law seems to make either of these origins untenable, but supports the view suggested here, that it was laid down during a very short halt of the Highland Ice which spanned the mouth of Upper Clydesdale, from Quothquan Law to the foot of Tinto, at Park Knowe.

It would then seem to follow that the Symington feature, a linear ridge of whose esker origin there can be no doubt, was the product of the Northern Ice as it gradually retreated northward from the place of parting with the Upper Clydesdale Glacier, about Symington. The heaps of sand and gravel near Lamington are possibly the deposits of the Upper Clydesdale Glacier.

The break between the Northern Ice and the Tinto Glacier probably took place between Faulburn and Blackleg. The Northern Ice, no longer confluent with the Tinto Glacier or the Upper Clydesdale Glacier, gradually receded in the direction of Carstairs. After shrinking back from the Stone, Whitecastle, and Carmichael Hills, this ice deposited its moraines, on the western side of the Clyde, along the hill slopes south and south-west of Pettinain, and on the eastern side, from near Liberton, by Gladstone, near Westend, across the South Medwin valley toward Newbigging and east of Kaim-end.

#### 6. *The Kame-moraines from Douglas to New Cumnock and the Retreat from the Hagshaw and Nutberry Hills.*

A kettle-moraine runs along the south side of the Douglas valley to Muirkirk, whence "there is a struggling line of kames"† on the moors to New Cumnock. At this period the ice apparently covered more or less completely the Hagshaw and Nutberry Hills, which extend northward from Muirkirk to the Irvine and Avon valleys. As in the case of the Pentland Hills, the thinning of the ice, consequent upon the retreat, caused an early emergence of the higher summits and the formation of two ice-lobes—the one, the "Airds Moss Lobe," thrust from the west into the Ayr valley to Muirkirk, the other extending up the Douglas Water, from the east or north-east. The marginal streams flowing along the north edge of the "Airds Moss Lobe" and the drainage of the ever-increasing ice-free area of the Hagshaw and Nutberry

\* *Scot. Geog. Mag.*, xxxi (1915), p. 475.

† *Mem. Geol. Survey*, Sheet 23 (1873), p. 44.



Hills carved a series of channels which were mapped in the course of this work, the writer at the time being unaware of the earlier investigations of Mr J. SMITH\* and Mr G. V. WILSON.† The reader is referred to these papers for details of these features. The highest was observed at an altitude of approximately 1300 feet O.D.

Moraines also abound in places to support the evidence of the drainage phenomena. At an early stage, as the ice fell away from the hills, conforming to their contours, it deposited the discontinuous series of kame ridges to the north of these hills, also those at an altitude of about 1200 feet‡ in the upper waters of the River Logan. Later moraines were noticed in this valley below 900 feet O.D., formed when the drainage, held up in the Kype Water, escaped by the "Snout" and the valley near Stockbriggs.

Along the north of the "Airds Moss Lobe" there was laid down the kame terrace which runs from the Whitehaugh Water at 1000 feet round Meanlour Hill to Greenock Water.§

The simultaneous shrinkage of its southern margin initiated the marginal drainage, e.g. the two well-marked channels noted by Mr E. M. ANDERSON|| and independently by the writer, which cross the watershed between the valleys of the Gass and Ayr. These drained north-eastward into "Lake Muirkirk," whose existence had already been inferred by J. GEIKIE.¶

"Lake Muirkirk" also received the Ponesk and other glacial streams, entering from the north. Sands and gravels, swept into the lake, are well displayed about Muirkirk. The lake waters escaped eastward into the Douglas Water, dissecting the earlier formed moraines and moulding them into their present form. The behaviour of the marginal drainage and moraines proves that the "Airds Moss Lobe" lingered longer than the "Douglas Water Lobe."

#### 7. *The Kame-moraines of the Rhinns of Galloway and Stranraer.*

At the period of maximum readvance, the Highland Ice over South Ayrshire, west of New Cumnock, was confluent with the local glaciers of the Southern Uplands. Moraines of this stage are in consequence absent. Where, however, as round Loch Ryan, a free edge of the Northern Ice again occurs, the moraines are as conspicuously displayed as on any other section of the ice-front.

The moraine sweeps round the head of Loch Ryan as a broad, hummocky belt, south of Stranraer. It spreads under the grounds of Castle Kennedy on to the foot of the hills east of Loch Ryan, becoming much less conspicuous as it is traced northward beyond Strandmain. Its billowy surface is especially well seen east of Intermessan, south of Drummuckloch, and along the western edge of Castle Kennedy grounds. Though it forms virtually one great morainic belt, it is possible to single out individual ridges swinging across the wide depression from side to side.

With free outfall for the glacier streams, a great outwash plain was spread out to the south, grading imperceptibly into the 60-foot beach. The boundary between the outwash and the beach is difficult to map, but may run from Planting End by Barnoltoch and Kildrocht.

This great accumulation has in the past been assigned to the 100-foot beach.\*\* The chief reasons for interpreting it as a kame-moraine with outwash are the following:—

First, the billowy and kettle-studded surface—which is characteristically morainic; had the deposit been 1000 feet above sea-level instead of 100 feet, few doubts would have been entertained of its morainic origin.

\* *Trans. Geol. Soc. Glasgow* (1896), p. 331.

† *Mem. Geol. Survey*, Sheet 23 (1873), p. 44.

‡ *Great Ice Age*, 3rd ed. (1894), p. 179.

+ *Summary of Progress for 1921* (1922), pp. 80, 81, and map, fig. 3.

§ *Ibid.*

|| *Summary of Progress for 1923* (1924), p. 105.

\*\* E.g., *Geol. Survey of Scotland*, Sheet 3 (1923).

Secondly, the southerly direction of the stratification throughout the deposit, which in the more northerly parts seems inconsistent with the beach origin.

Thirdly, the occurrence of the wings of the deposit at elevations above those usually regarded as the maximum altitudes for the late-glacial sea-level.

Fourthly, the passage to the north-west, about Leswalt, into undoubted moraines, occurring up to 300 feet or so above sea-level.

Fifthly, the difficulty in initiating such a beach. The tidal scour through this strait, across the site of the present isthmus, were Loch Ryan and Luce Bay continuous, would effectually prevent the formation of such a beach, though its preservation, once formed, would be an easy matter, as seen in the present conditions. It seems necessary to assume, therefore, that the sea which late-glacially again entered the lochs to north and south found no through passage. The erection of a moraine across the strait would secure this.

Sixthly, the existence of a marginal channel, falling south across the hill spur at an altitude less than 500 feet O.D., east of Laffnolls Point; it drained a lake impounded in the Beoch Burn. Though this valley does not prove a halt of the ice on the line of the Stranraer moraine, it does seem to show that the last ice in this region was receding northward out of Loch Ryan, when conditions might arise favourable to the origin of a moraine in this area.

An early stage of the Stranraer moraine is represented by the large kame-moraine spanning the valley of the Water of Luce at its mouth.

Moraines corresponding to those at Stranraer were observed in the Rhinns of Galloway. One joins the Stranraer moraine, near Leswalt, and runs by Lochnaw Castle to Balgracie, east of Knockaldie and south of Portslogan; here it holds up the bog to the east. The sands and gravels near Portpatrick Station, containing streaks of coal fragments, are probably of the same date. A later stage is represented by the sands and gravels beneath Galdenoch Moor, which cause the stagnant drainage of Glengyre and Garchie Moss to the east. This material also underlies, as a kame-terrace, Larbrax Moor, the sands showing water action from the north or north-west.

Similar features occur at intervals inland from the west coast of the Rhinns, further south, *e.g.* those curving to the south-east from Little Pinminnoch. Outwash materials also occur in places, *e.g.* east of Pinminnoch Burn, at Bog End, and west of Colfin.

These great moraines have now been traced from coast to coast, from Dunbar to the Rhinns of Galloway. The only break of any magnitude is in South Ayrshire, between the Nith and Loch Ryan, where the Highland Ice was in immediate contact with the glaciers from the Southern Uplands.

It is now proposed to sketch briefly the larger stages of the recession of the ice-sheet and the different phases of the dissolution of the Highland Ice in the southern part of the Central Valley of Scotland.

#### 8. *Retreat from the Northern Flanks of the Pentland Hills.*

It has been shown that the ice which overrode the Pentland Hills broke up, by thinning, into two ice-lobes—an "Esk Lobe" and a "Dolphinton Lobe"—retreating toward the Forth Estuary and Carstairs respectively. Simultaneous melting caused the ice to fall away from the northern slopes of the Pentland Hills.

The moraines east of Carnwath continue to Easter Yardhouse and the Kames, and east of Tarbrax to Crosswoodhill and the Roman Camp. During one phase they were laid down at intervals along the flanks of the hills to the east and about this altitude. They are shown



about Harperrigg Reservoir and Cairns Castle, in the hollow west of Bavelaw Castle\* and near Threipmuir Reservoir. At a slightly later stage they were continued from the Roman Camp to the east of Linhouse Water, to Corston and Kirknewton, and along the north-east slopes of the Pentland Hills.

A later position, though still, generally speaking, part of the same great morainic phase, is represented by the moraine which runs from the Carstairs moraine along the Dippal Water by Ampherlaw and the western side of Stallashaw—this moss is held up by moraines to east and west—to Harburn, continuing along the Linhouse Water to Kirknewton, and by Currie and Colinton to the Braid Hills. The Comiston boulder † lies within it.

Over the whole of this stretch the materials are of composite origin and character; in part they are morainic, in part overwash and lacustrine—as above Colinton, near Murrayfield, and above Roslin.

The marginal drainage at the west end of the Pentland Hills, *e.g.* the small channel north-east of Carnwath, escaped into the Medwin and the Lyne Water, at the east end into "Lake Esk," *e.g.* the channels along the flanks of the Braid Hills.

#### 9. The Carstairs Kame-moraine.

This kame-moraine has been so frequently and so fully described that it would seem that no contribution of any value could be made to our knowledge of it. It is here indeed unnecessary to do more than make reference to the earlier literature upon it, ‡ and to discuss the question of its origin.

Since it spans the exit from Upper Clydesdale, it has been generally—indeed, apart from the earlier writers as R. CHAMBERS § and D. MILNE HOME, || the one considering it a raised beach, the other a submarine bank—unanimously regarded as the moraine of a large glacier debouching upon the plain of Lanark from Upper Clydesdale. ¶ This view seems to be confirmed by the apparent convexity to the north and by the contents of the moraine, which are chiefly local or from the Southern Uplands. The chief constituents, expressed in percentages, as computed by Professor GREGORY,\*\* are quoted here :

Old Red Sandstone felsite and porphyry . . . . .	34 per cent.
Old Red Sandstone . . . . .	30 "
Southern Upland greywackes . . . . .	30 "
Carboniferous Sandstone . . . . .	3 "
Highland rocks . . . . .	2 "
Basalt . . . . .	1 "
	<hr/>
	100 "

In the face of this apparently overwhelming evidence the writer contends that the Carstairs moraine was formed, not by a glacier issuing from Upper Clydesdale, but by Northern Ice of Highland origin. The nature of the evidence is as follows.

Professor GREGORY has maintained †† that this feature is not continued to Cleghorn and Lanark, as was earlier asserted by Sir A. GEIKIE, ‡‡ but that the sands and gravels in these localities are due to the denudation of fluvio-glacial sheets. He also contended that its

\* B. N. PEACH, *op. cit.*, p. 146.

† A. C. CAMPBELL and E. M. ANDERSON, *Trans. Geol. Soc. Edinburgh*, ix (1909), p. 219.

‡ J. W. GREGORY, *Scot. Geog. Mag.*, xxxi (1915), pp. 465–476, with references to literature.

§ *Ancient Sea Margins*, 1848, p. 213.

|| *Trans. Edinburgh Geol. Soc.*, iv (1881), p. 69.

¶ *E.g.*, J. GEIKIE, *Great Ice Age*, 3rd. ed. (1894), p. 187; J. W. GREGORY, *op. cit.*, p. 473.

\*\* *Proc. Geol. Assoc.*, xxvi (1915), p. 161, footnote.

†† *Scot. Geog. Mag.*, xxxi (1915), p. 474.

‡‡ *Mem. Geol. Survey*, Sheet 23 (1873).

extension to the east is likewise strictly limited and independent of the Stallashaw kames, which occur in the upper part of the North Medwin valley at a height of 850 to 900 feet and south-east of Stallashaw Moss. These features, he says, appear to have been formed by a glacier which descended from Harrows Law at the south-west end of the Pentland Hills. This view is at variance with the older one,\* that the Stallashaw kames were continuous with the Carstairs moraine, the whole trending south-west. It is difficult to understand why Harrows Law, whose summit is only 1360 feet and devoid of any large gathering ground, should have nourished a local glacier which could descend through a vertical distance of 400 to 500 feet and flow over a horizontal distance of some two or more miles, when, so far as the writer's reading † and knowledge of the ground extends, there is no trace of a local glaciation elsewhere in the Pentland Hills, though some of the summits possess an elevation exceeding that of Harrows Law by about 500 feet. Moreover, during this research no difficulty was found in tracing the physical connection between the Stallashaw kames and those of Carstairs. It seems necessary, therefore, to return to the older view, and to consider these features as parts of one deposit.

West of Carstairs the moraine can be just as readily followed to Douglas, as was noticed by Sir A. GEIKIE.‡ Professor GREGORY circumvents this continuity by first denying the morainic origin of the sands and gravels about Lanark, and secondly by interpreting the mounds south of that place as drumlins. With regard to these, it is difficult to see what ice could have formed them if they be considered as drumlins. Their trend, north-east south-west, is clearly inconsistent with a flow of either Highland Ice or the Upper Clydesdale Glacier. The contention that they are the product of a Douglas Water glacier flowing north-east, as suggested by Professor GREGORY,§ is again totally at variance with the evidence of the glaciation of the Hagshaw and Nutberry Hills by ice from the north (*cf.* p. 32 above), and with the existence of "Lake Muirkirk" (*cf.* p. 33 above) now indisputably proved, and lastly, with the lakes in the valleys south of Muirkirk (*cf.* p. 33), in which the Douglas Water glacier would presumably have its roots. These so-called drumlins are not true drumlins, but moraines.

It has been shown in earlier sections that the Northern Ice laid down the great kames in the Douglas Water and north of the Pentland Hills, *i.e.* to west and east respectively of the Carstairs moraine. It has been the aim of the last two paragraphs to show that these features are perfectly continuous with the Carstairs moraine. It seems, therefore, logical to conclude that this, like those, was also the product of the Highland Ice advancing from the north; the ice was on the north of the moraine.

This view is borne out by the fact, noted by Professor GREGORY,|| that the north face of the Carstairs kames is best defined where it rises steeply from the alluvial flats of the Mouse Water. "The southern margin," to quote Professor GREGORY, "is less regular, and the kames pass gradually into the inter-kame sands." This undoubted behaviour points irresistibly to a northern glacier with the steep ice-contact face to the north and the overwash sands, with their gradual slopes, to the south.

The small drainage channels, falling south, near Westhall and Weston (both east of Carstairs) imply ice-pressure from the north.

Corroborative evidence is furnished by the retreat moraines of the Clyde Glacier (p. 40); it may be appreciated at this point by reference to the map. If the Clyde Glacier, in

\* Sir A. GEIKIE, *ibid.*, p. 43.

† *Mem. Geol. Survey*, Sheet 32 (Edinburgh), 1910, p. 324; a contrary opinion was expressed by J. D. BROWN, *Trans. Edinburgh Geol. Soc.*, II, pp. 133, 251.

‡ *Op. cit.*, p. 44.

§ *Scot. Geol. Mag.*, xxxi (1915), p. 473.

|| *Ibid.*, p. 470.



inverse order to the actual sequence of events, be imagined as expanded from its Eaglesham-Carluke stage (a mere inspection of the map suffices to show the correctness of this correlation), on its western side to the line of the Irvine-Avon moraine, on its eastern side to the Pentland moraine, it will readily be seen that the snout of the Clyde Glacier would be thrust forward to the position of the Carstairs moraine.

Incidentally, it is impossible to interpret the Thankerton moraine, stretching across the Clyde valley, as the product of the Tinto Glacier, as Professor GREGORY has done, if the Carstairs moraine, situated north of this, is the moraine of the Upper Clydesdale Glacier itself, without postulating a readvance of the Tinto Glacier into the valley of the Clyde, vacated by the Upper Clydesdale Glacier. Such a readvance was neither proved nor apparently suspected by Professor GREGORY. The interpretation of the Thankerton moraine given above (p. 32) is, however, consistent with the general views of the origin of the Carstairs moraine here presented.

Though from the above arguments a northern origin seems incontestable, there remain two obvious and apparently weighty objections which must now be considered. The first, and the one which offers the least difficulty, is the convexity to the north. When the moraine from the Pentland Hills to the Douglas Water is considered as a whole, it is seen to be concave to the north, with only a slight convex indentation in the middle of its course (see map). This convexity over the shorter distance may be explained by ascribing it to the melting action on the ice of waters from the south. This explanation has already been adopted by Mr G. W. LAMPLUGH for the Bride Hills of the Isle of Man.\*

In the case of the Carstairs moraine the apparent convexity would be considerably reduced, if not entirely removed, were the huge accumulations restored which doubtless once filled the area between Pettinain, Carstairs, and Lanark, which were removed by the post-glacial Clyde and by the current in "Lake Clyde," when its surplus waters escaped into the Tweed by Biggar Gap (see below) during the prolonged retreat of the Highland Ice down the Clyde, prior to the escape by the Bonny Water into the Forth.

The second objection is concerned with the composition of the moraine. While the high percentage of O.R.S. materials is not critical, being local and therefore reconcilable with ice-flow from any direction, the large percentage of Southern Upland rocks presents more difficulty. This may, however, be accounted for in several ways. As is generally accepted, powerful ice-masses poured out of Upper Clydesdale for much the greater part of the Glacial Period, bearing immense quantities of southern material with them. The boulder-clays north of the embouchure of the Upper Clyde must, in consequence, have been heavily charged with this debris. Northern Ice advancing over this boulder-clay during the readvance postulated in this paper would, as has so often been shown in glacial literature, incorporate much of this older deposit in its lower layers, redepositing it on its melting as morainic and fluvio-glacial materials.

To this method may be added a second. When, at the period of maximum readvance, the Highland Ice and the Upper Clydesdale Glacier were confluent, any variations in their relative strengths would induce oscillations northward and southward, so that the local glacier might carry its southern erratics north of the line of final parting, which has been placed well to the south of the Carstairs moraine.

A further possibility may be indicated. When the Highland Ice stood on this line, the accumulations heaped up in front of its receding edge would include not only material washed out of the ice, but also southern debris transported northward by the River Clyde. Professor KENDALL and Mr BAILEY have indeed proved that along the north of the Lammermuirs a high percentage of the materials is of southern origin, and though the conditions are by no means

\* *Mem. Geol. Survey*, "Geology of the Isle of Man" (1903), p. 397.

identical, this northward carry by stream action may here have contributed on a small scale to the large quota of southern rocks at Carstairs.

It is therefore suggested that by incorporation in the lower layers of the advancing Highland Ice of material from the older boulder-clay of Southern Upland origin and its redeposition, by the washing of this boulder-clay by melt-waters from this ice during the readvance, by oscillations of the Upper Clydesdale Glacier and the Highland Ice at the time of maximum readvance, and probably, quite auxiliary, by contributions from the southern rivers when the Northern Ice stood at Carstairs, the large proportion of Southern Upland rocks may be satisfactorily explained. Though these different reasons, taken together, may be regarded as adequate, it is impossible to assign relative importance to each of them.

The Stallashaw moraine, in composition not greatly dissimilar from the one at Carstairs, yet doubtless of northern origin, would appear to lend additional support for this view.

The small percentage of Highland rocks at Carstairs does not militate against the view of the northern origin, for elsewhere, where the ice was partly of Highland origin, the proportion of these rocks has been similarly small. Thus only 2 to 5 per cent. of Highland material occur in the drifts of the lower part of the Firth of Forth,\* and a few pebbles only were found near Comiston.† Professor GREGORY‡ has suggested the derivation of these erratics at Carstairs from an older boulder-clay. It is here contended that they are directly derived, while the southern constituents were obtained from an older drift.

The pieces of Coal Measure Sandstone and coal fragments, which Professor GREGORY§ says are doubtless from the Douglas coalfield, may, with equal probability, be referred to the Lanarkshire coalfield to the north-west.

#### 10. *Retreat from the Valleys of the Irvine and Avon.*

An important stage in the ice-retreat is represented by the series of moraines which skirt the south sides of the Irvine and Avon valleys. They extend from south of Galston, north of Changue Hill and Mill Rig, around Glengavel, by Kypes Rig and Black Hill to near Lesmahagow, continuing at one stage as the sands and gravels stretching southward from this place as far as the Douglas Water. A large ice-lobe, thrust southward up Glengavel, formed an extra-glacial lake, which drained south by a direct channel into the Greenock Water and "Lake Muirkirk."

At this period the ice-sheet was probably continuous, though thin, over the moorland extending from the Irvine and Avon northward to Eaglesham and the Clyde valley. Progressive thinning and recession rapidly resulted in the break-up of this ice into two lobes—the one thrust from the east or north-east, continuous with the Clyde Glacier, and occupying the Avon for a short distance west of Strathaven, the other, in possession of the Irvine valley as far as Newmills and protruding from the ice-sheet over Ayrshire.

Great spreads of materials on the watershed between the Irvine and Avon, *e.g.* near London Hill,|| were laid down in this lake; their dip and stratification indicate a stream flowing from the west.

Later lowering of the lake-waters led to the cutting into these lake deposits¶ of a channel—the "Windy Wizen"—falling east. It would appear, therefore, that the eastern lobe withdrew more rapidly than the western one; the drainage was carried into "Lake Clyde."

\* Sir A. GEIKIE, *Text-book of Geology*, ii (1903), p. 1310.

† *Scot. Geog. Mag.*, xxxi (1915), p. 470.

‡ J. SMITH, *Geol. Mag.* (1900), p. 142.

¶ *Ibid.*, *Trans. Geol. Soc. Glasgow*, xi, Supplement (1898), p. 60.

+ *Trans. Edinburgh Geol. Soc.*, ix (1909), p. 219.

§ *Ibid.*, p. 470; *Proc. Geol. Assoc.* (1915), p. 161.



A further slight retreat, chiefly a withdrawal of the ice out of the Avon valley, begins the story of the recession of the western margin of the Clyde Glacier (p. 42).

#### 11. *The Kame-moraines of South and Central Ayrshire.*

In the vicinity of Maybole occurs a series of tumultuous morainic mounds.\* West of Maybole they are thrust into the gap giving access to Culzean Bay and are readily traceable as far west, at least, as Pennynglen. In the larger glen, followed by the Kirkoswald road, they are also well displayed, filling the whole of the gap west of Kirkoswald, and resting against the flanks of the hills on either side of it. To the south they rise on to Knockbrake and curve along its edge into the Girvan Water, where they are traceable down the valley to Bargany, though they are better shown near New Dailly.† Farther north they occur about Kilkerran. From the moraines in the Girvan Water, where the ground sloped away from the ice, outwash gravels extend in the direction of Girvan; in the gaps west of Maybole, where the slope was toward the ice, lakes were impounded, the drainage escaping westward by well-marked channels.

Moraines of slightly later date occur east of Maybole; they were traced to Dynock Burn.

The "Lammermuir-Stranraer Moraine" is absent from South Ayrshire, as noted above. With the "Pentlands-Carstairs-Galston Moraine" are to be correlated the Maybole moraines, when glaciers issued from the Doon and Lugar Water, and when the marginal mounds of Holybush Station, Sandhill, Bogside, and near Ochiltree‡ (probably later) were laid down.

The manner of the later recession from South and Central Ayrshire is difficult to ascertain. The Doon and Lugar Water glaciers doubtless shrank southward up the valleys, while the Highland Ice withdrew northerly or north-westerly, its edge swinging off the coast and out to sea in a series of crescentic curves, as on the east coast, south of Dunbar.§ This reconstruction is suggested by the occasional moraines noticed in this coastal strip, *e.g.* near Auchencroch, near Bennane Head, north of Ballantrae and of Girvan, and near Culzean Castle. The small dry valleys south-east of Downan Point also indicate the presence of ice out to sea. Some of these coastal moraines probably belong to the stage of the Maybole moraines, when the Highland Ice, united with the Doon Glacier, swung into the Girvan Water valley, round the hills south of Ayr, and out to sea.

#### 12. *The Parting of the Forth and Clyde Glaciers.*

To satisfy myself that the moraines extending from the neighbourhood of Edinburgh along the north of the Pentland Hills to Carstairs and the valleys of the Avon and Irvine were truly contemporaneous and not merely an agglomeration of moraines of diverse ages, it was deemed advisable to investigate the retreat phenomena of the Central Valley. The results of this inquiry, embodied in the following brief account, confirm, it is submitted, the general truth of the sequence of the events which have been set out.

As the ice-sheet in the Central Valley was fed in the main by glaciers flowing along the depressions of the Forth and Clyde, any thinning, consequent upon retreat, would cause the ice to split into its component valley glaciers. This tendency would be especially pronounced in the lee, *i.e.* to the east of the Campsie Fells and Kilsyth Hills. It is therefore not surprising to find that the plateau stretching northward from Bathgate to the Forth was the first area vacated by the ice. This upland became ice-free by the falling away of the Forth Glacier

\* *Mem. Geol. Survey*, Sheet 14 (1869), p. 25.

§ P. F. KENDALL and E. B. BAILEY, *op. cit.*, p. 16.

† *Ibid.*

‡ *Ibid.*

northward and the Clyde Glacier westward. Occasional morainic mounds, *e.g.* between North Coulston and Crawshaw Hill and in the area of Bangour Asylum, indicate the first stages of its dissolution.

The southern edge of the Forth Glacier was marked at one important stage by the Polmont kame, which has been fully described.\* It seems to extend as far eastward as Winchburgh, and even to Kirkliston, passing into outwash material. Traces were also recognised about Queensferry. Of slightly later age, probably, are the sands and gravels of Denny, while of somewhat earlier date, and marking the cleavage in the lee of the Campsie Fells, are the mounds † on the watershed between Bannockburn and Buckie Burn at 1000 feet.

The ice north-west of the Pentland Hills shrank back during the period of lowering of the ice, north of Bathgate, to form a lobe extending eastward from the Clyde. Its northern margin at an early stage is fixed by the mounds near Slamannan, at a slightly later stage by the moraines skirting the hillside from the west of Blackridge by Armadale to Bathgate, where they expand into the depression leading to Linlithgow, as terrace-like spreads of sand and gravel, ‡ continuing eastward to Livingstone. Here apparently the ice-front curved across to the western part of the kettle-moraine east of West Calder.

The outwash plains west of Edinburgh, *e.g.* near Gogar and Corstorphine, are probably of the same age, formed by the melt-waters from the ice of the stage of the Polmont and Bathgate moraines; the finer muds were carried to a greater distance, and may be represented in part by the Portobello clays.

Retreat stages from the Bathgate position are given by the moraines running from Tashyburn, by Haywood to Burnfoot, and by those near Wilsontown, south of Stobwood and near Craighenhouse, all formed as the ice withdrew from the plateau between Carstairs and Bathgate. Of about the same age are the mounds south of Fauldhouse and on the Fauldhouse Hills, and those which swing tangentially out of the Bathgate moraine, the one curving from this moraine about three or four miles west of Bathgate to near Whitburn, the second from Blackridge, by Netherton to Harthill and beyond.

These show that along the eastern side of the extended Clyde Glacier the ice was thrust eastward into the depressions north and south of Polkemmet Moor in more or less close conformity with the relief, and that it retreated earliest from the uplands.

By these clearly marked stages the shrinkage of the ice into a huge glacier filling the Clyde valley was effected.

### 13. *Retreat of the Clyde Glacier.*

The moraines of the Clyde Glacier are disposed in loops, having for their axes the central line of the valley. The moraines of the east side will now be briefly sketched; the description of the western edge will follow.

#### (a) *The Eastern Margin.*

The eastern margin fell along the hillsides from about the latitude of Shotts and the Kirk of Shotts northward, and, judging by the marginal channels, fairly rapidly, to the valley of the Bonny Water, southward to the Clyde, below Lanark. In this direction the position is given by the moraine which can be traced at intervals from Cartland—this may be slightly earlier—to Carluke, Hyndshaw Row, near Blackhall and Darngavel Farm, Stane, and the Kirk of Shotts.

\* Cf. J. W. GREGORY, *Trans. Geol. Soc. Glasgow*, xiv (1912), p. 212, where references to the earlier literature will be found.

† *Mem. Geol. Survey*, Sheet 31 (1879), pp. 51, 52.

‡ *Ibid.*, Sheet 32 (Edinburgh), 1910, p. 332.



A moraine of slightly later date runs from the west of Law Hill (north-west of Carluke) to Bogside, Morningstone, east of Bonkle to Allanton and Stane,\* and into and around the Shotts valley. Of this age are the marginal valley, noted about four miles east of Airdrie, below 700 feet, and the moraine one mile west of this. Northward from here the marginal features become much less distinct until the region of the large overflow valleys, falling into the Bonny Water, is entered. The first of these intakes at about 500 feet and falls north from Riggend to near Glenhouse. A later one, in parallel sequence, intakes at a slightly lower level, about one mile west of Riggend, and was drained northward—at one stage into the valley falling to Luggiebank. The corresponding moraine runs west of this by Cumbernauld House to Castlecary, across the Bonny Water about Hollandbush, and then westward to Kilsyth. This proves that an ice-tongue was thrust eastward from the Clyde Glacier into the gap extending eastward from Kilsyth. At this stage the Forth Glacier had retreated to above Falkirk, and the drainage from the "Kilsyth Lobe" escaped into the Forth. Its outwash materials were spread by Bonnybridge and merged into the 100-foot beach; much of the so-called 100-foot beach in this neighbourhood is well above this level† and is quite destitute of shells; its fluvio-glacial origin seems clear. The 100-foot beach, *in sensu stricto*, west of Falkirk, was apparently largely derived from the flood waters of the melting "Kilsyth Lobe." This outwash material was later modified by overflow waters of the lake, subsequently impounded to the west by this retreating lobe.

Professor GREGORY‡ has regarded the Polmont kame as marking the southern edge of the Forth Glacier and yet as continuous from Falkirk to Kilsyth in the west. The suggested distribution seems incompatible with the suggested origin, for at Kilsyth the moraine would be separated from its glacier by the width of the Kilsyth Hills. It would appear more comprehensible to regard the portions east and west respectively of Falkirk as of different origin, the one marking the southern edge of the Forth Glacier, the other as the product of the receding "Kilsyth Lobe" of the Clyde Glacier.

The free outlet of the drainage from this lobe shows that the Forth Glacier at this time was halted above Falkirk. Since with this halt there would be associated a moraine of the dimensions of that described in connection with the "Kilsyth Lobe," and since, moreover, no moraine of this kind occurs below Stirling, it appears reasonable to assume that the moraine at this place is of the same age as the marginal features of the "Kilsyth Lobe."

The correlation of the Stirling moraine of the Forth Glacier with the moraines of the "Kilsyth Lobe" of the Clyde Glacier clearly implies the contemporaneity at an earlier stage of the Polmont kame with the Bathgate moraine; a study of the map shows the probability of this correlation. Such correlations, definitely implying a greater extent of the Clyde Glacier as compared with the Forth Glacier, are in agreement with the known predominance of the western ice in the Highlands during later phases, and with its greater extent at earlier periods, as suggested by the "Lammermuir-Stranraer Moraine" and the behaviour of the ice-lobes to east and west of Muirkirk and of those in the Irvine and Avon.

A channel, later than the one at Riggend, intakes below 400 feet, east of Glenboig. This and the higher channels carried the drainage, firstly, into the valley followed by the railway at Cumbernauld Station, and later into that which runs north-easterly to Cumbernauld. Another small valley occurs south of Craighalbert. The moraine of this date is traceable from about Condorrat in the direction of Kilsyth.

\* *Mem. Geol. Survey*, Sheet 31 (1879), p. 51; *ibid.*, "Central Coalfield of Scotland," vi (1923), p. 119.

† *Ibid.*, p. 53.

‡ *Trans. Geol. Soc. Glasgow*, xiv (1912), p. 199.

The absence of overflow channels south of Airdrie at lower levels than those just described is another proof of the drainage of "Lake Clyde" by Biggar Gap.

(b) *The Western Margin.*

A prolonged halt was made on the line now marked by the moraine with steep face to the north, which runs from south of Eaglesham, west of Cleuchern Lodge, by Cladance, and south of Chapelton.\* Mr C. DINHAM noted marginal drainage features in association with it.† South of Chapelton the line continues east of Strathaven, across and along the Avon valley, south of Stonehouse and by Blackwood, curving round to the Clyde near Nemphlar, where it joins with the moraine on the eastern side of the valley at Cartland.

A later line, following a slight retreat apparently of the snout of the glacier only, can be traced by the moraine running from Chapelton, by Glassford, West Quarter, to the south of Stonehouse. It probably continued, though its course was not indicated by anything which could be recognised in the field, by about Crossford to the Carluke moraine.

A younger moraine runs approximately one and a half miles north of the Chapleton-West Quarter moraine to the north of Stonehouse, whence the ice-front curved across the valley on to the western side of Law Hill.

A later stage is given by the moraines extending westward for about three miles from West Quarter. Its continuation on the east of the Clyde is presumably to be sought along the hillsides in the vicinity of Airdrie.

Later stages are indicated by the floor deposits of "Lake Clyde,"‡ stretching from Hamilton to the north of Larkhall,§ and a still later one by the mounds extending from Broomhouse and Daldowie by Reddawood and Hallside to the flanks of Dechmont Hill. During a retreat from this line a subglacial stream laid down the esker ridge running from Tollcross by Vermont and Broomhouse.||

Though signs of the succeeding retreat are by no means numerous, the occurrence of overflow channels, draining the extra-glacial lakes on the western margin of the Clyde Glacier, e.g. the Lugton valley,¶ and their absence from the southern slopes of the Renfrew Hills, proves that the Clyde Glacier lingered longer than the ice covering the lower parts of North Ayrshire.

14. *Retreat from Fife and Kinross.*

A well-defined position of the ice-margin in Fife and Kinross is given by the belt of moraines extending from the southern shoulder of the Lomond Hills by Leslie, Markinch,\*\* and Kennoway to the north of Largo and Colinsburgh,†† and finally merging into the raised beaches of the Firth of Forth along the stretch from Leven to St Monance.

To the north of the Lomond Hills the moraine runs from the northern shoulder to the south of Falkland and the area around the New Inn, whence it continues along the side of the hills bounding Stratheden on the south, attaining the coast of Fife in the neighbourhood of Kingsbarns and Boarhills.‡‡

\* E.g., *Mem. Geol. Survey*, Sheet 22 (1872), p. 29; J. GEIKIE, *Great Ice Age* (1894), p. 177; J. W. GREGORY, *Trans. Geol. Soc. Glasgow*, xiv (1913), p. 214.

† *Summary of Progress for 1923* (1924), p. 106.

‡ J. W. GREGORY, *Trans. Geol. Soc. Glasgow*, xiv (1913), p. 314.

§ *Mem. Geol. Survey*, "Econ. Geology of Central Coalfield of Scotland," vii (1920), p. 132.

|| "Geology of the Glasgow District," *Mem. Geol. Survey*, 2nd ed. (1925), p. 227.

¶ J. GEIKIE, *Great Ice Age*, 3rd ed. (1894), p. 122.

\*\* *Mem. Geol. Survey*, "Central and Western Fife and Kinross" (1900), p. 185.

†† *Mem. Geol. Survey*, "Geology of East Fife" (1902), p. 296.

‡‡ *Ibid.*



At this period, when the ice abutted against the steep western side of the Lomond Hills to an altitude exceeding 1000 feet above sea-level, the lower Benarty and Cleish Hills and the equally high Ochil Hills, which lay farther westward in the path of the rapidly thickening Highland Ice, were apparently buried beneath this extraneous mass. The Tay Glacier at this time was confluent with the large lobe in occupation of Stratheden, which swept eastward along the northern flanks of the Lomond Hills. This stage is doubtless to be correlated with the "Pentland-Galston-Maybole stage."

The further recession from this position in Fife and Kinross can be readily followed and had three important consequences—firstly, by the emergence of the relatively low hills south of the Motray Water, the separation of the Tay and Stratheden Glaciers; secondly, the emergence of the Ochil Hills, in places possibly crowned by small corrie glaciers, and as the ice fell away from the south-eastern slopes of these hills the progressive delimitation of the western margin of the Stratheden Lobe; thirdly, the appearance above the ice of the Benarty and Cleish Hills and the resulting cleavage of the ice in the east.

The shrinkage of the Tay Glacier exposed the summits of the higher hills between the Firth of Tay and the Motray valley—*e.g.* Glenduckie Hill (784) and Norman's Law (936)—and caused small lobes of ice advancing from the north-west to lap over into this valley. The larger of these was thrust between Glenduckie Hill and the hills south of Newburgh, and formed along its margin and during its retreat the kames which extend from the vicinity of Lindifferon by Glenbuckie and Glenbeg to Lindores and Lindores Loch,\* and later along the valley north-westward to Newburgh. A second tongue of shorter duration was protruded east of Norman's Law to the vicinity of Luthrie Station. The outwash materials distributed over the floor of the Motray valley, as far east as Kilmany,† are largely the product of the streams from the melting Lindores lobe.

The marginal accumulations, including moraine and outwash, heaped up about St Fort House, North Straiton, Wormit, and Crumblie Hill,‡ and marking the fanning of the Tay Glacier south-east of Dundee, together with the moraines on the hillside at Gauldry, are likewise of this age. They were laid down on the edge of the Tay Glacier as it fell away from the hills east of Kilmany, and are contemporaneous with the moraines of the Stratheden Glacier.

The line of moraines bordering the Firth of Tay east and west of Newburgh denotes a later stage.

The more important phases of the withdrawal of the Stratheden Glacier are indicated by the moraines which border this valley—on the north, from west of Milnathort, by Gateside, Auchtermuchty, Collessie, Cupar, and beyond; on the south by Pitlessie, Freuchie, and Falkland, the moraines swinging from the margin in large curves across the floor of Stratheden, *e.g.* about Leuchars Junction, Daisiemuir, Cupar, east of Ladybank, west of Strathmiglo, at Gateside, and Milnathort. The floor of Stratheden between these moraines is covered with outwash and overwash materials.§

The mode of retreat of the ice south of the Lomond Hills was in some measure controlled by the obstruction offered by the Benarty and Cleish Hills; the higher parts of these hills rapidly emerged above the surface of the ice, and with its progressive thinning caused an ever-increasing resistance to the flow and a parting of the ice in their lee. Moraines laid down under these conditions were observed at Kinglassie, east of Kirkness, and about Ballingry and Lochore.

Evidence of the manner of retreat from the plain of Kinross is furnished by the moraines

\* "Geology of East Fife," *Mem. Geol. Survey* (1902), p. 297.

† *Ibid.*

‡ *Ibid.*, p. 296.

§ *Ibid.*, p. 297.

flanking the Lomond Hills on the south-west and the Benarty and Cleish Hills on the north. Lacustrine, outwash, and overwash materials floor the plain of Kinross, while true esker ridges, e.g. those east of Balado Station, indicate the position of the subglacial streams.

A later pause in the retreat of the Kinross lobe in the direction of its parent glacier—the Forth Glacier—is evidenced by the marginal accumulations north-east and south respectively of Cull Hill and those near the Crook of Devon, while probably to this date are to be assigned the kames which extend eastward from Dunfermline to Crossgates and the Moss of Morran,\* and the overwash sands and gravels spreading in the same direction toward Lochgelly. This line, fixing the northern edge of the Forth Glacier at this stage, is without doubt to be correlated with the Polmont kame at a time when the snout of the Forth Glacier lay apparently slightly east of the site of the Forth Bridge. As the southern margin of the Tay Glacier at this stage is possibly to be regarded the Abernethy-Newburgh moraine; its equivalent north of the Tay was not investigated.

#### IV. EVIDENCE OF THE READVANCE ORIGIN OF THE "LAMMERMUIR-STRANRAER MORaine."

The attempt will now be made to prove what in previous sections has been assumed, that the "Lammermuir-Stranraer Moraine," stretching from south of St Abb's Head to the Rhinns of Galloway, with the important and significant break in south and central Ayrshire, marks the limit of a readvance of uncertain yet probably considerable magnitude.

The southern limit of the Highland erratics in Ayrshire and Lanarkshire is roughly coincident with the line of the moraine. These fragments have been noticed by earlier workers, and have been carefully observed during this investigation.

Small fragments of gneiss and schist occur in the drifts of Glenmore, Guelt,† and the Gass Water, in Glengaber,‡ at Chapelhouse in the Greenock Water,§ occasionally in the Ayr—e.g. near Sorn and at Barskimming||—in the Lugar and Douglas Waters, in the Carstairs moraine, and at Lesmahagow, sporadically in the drifts west of this town,¶ in the Irvine and Avon,\*\* over the Strathaven Hills, south-east of the Pentland Hills, and in east Lothian as far south as Tynehead, south of Ayr and toward Maybole, and in the moraines of Stranraer and the drifts of the Rhinns of Galloway. Here, and near the eastern end of the line, i.e. the eastern part of the Lammermuirs, the Highland erratics pass beyond the limits of the moraines; their transgression of the line at either end is due to the earlier glaciation, which here attained more southerly latitudes than at the stage under discussion.

A distribution, somewhat similar, has been observed in the case of the shelly drifts. Mr J. SMITH has contributed the greater share to our knowledge of these drifts; his records have been checked and extended. The shelly drifts occur very widely distributed in central and north Ayrshire. They were found in all the streams draining southward into the Irvine and in the Ayr; between Garvel and Strathaven to 700 feet above sea-level,†† at 1330 feet north-east of Muirkirk in the Leaze Burn,‡‡ in the Douglas Water at 1060 feet and for a distance of two miles downstream,§§ in the Guelt Water up to 900 feet,|||| in the Dippal Burn at 1060 feet,¶¶ in the Muirfoot Burn, New Cumnock, at 780 feet,\*\*\* and in the Water of Coyle at 920 feet.†††

\* Summary of Progress for 1923 (1924), p. 126.

† J. SMITH, *Proc. Liverpool Geol. Soc.*, vii (1900), p. 486.

‡ *Ibid.*, p. 27.

§ D. BELL, *Geol. Mag.* (1896), p. 335; *Mem. Geol. Survey*, Sheet 22 (1872), p. 23.

|| *Geol. Mag.* (1900), p. 142.

¶ *Brit. Assoc. Handbook, Glasgow* (1901), p. 521.

\*\* *Ibid.*, p. 80.

\*\*\* *Ibid.*, p. 69.

† *Mem. Geol. Survey*, Sheet 15 (1871), p. 38.

§ *Ibid.*, *Trans. Geol. Soc. Glasgow*, xi, Supplement (1898), p. 58.

|| *Mem. Geol. Survey*, Sheet 23 (1873), p. 42.

¶ *Ibid.* (1872), p. 23.

†† *Ibid.* (1902), p. 479.

‡‡ *Trans. Geol. Soc. Glasgow*, xi, Supplement (1898), p. 76.

|||| *Ibid.*, p. 76.



Mr J. WRIGHT obtained foraminifera from these drifts.\* During this research they have also been observed, among other places, in the lower reaches of the Garpel Water, south of Ochil tree, in the lower parts of the Doon, in the coastal strip of Ayrshire—*e.g.* south of the Heads of Ayr—at Dunure, Culzean Castle, south of Turnberry, at Girvan, Lendalfoot, Bennane Head, Ballantrae, in the Currie Burn, along both shores of Loch Ryan, all over the Rhinns of Galloway, and in the Stranraer moraine. These coastal occurrences, and those near Stranraer and in the Rhinns of Galloway, may date back to any part of the Glacial Period after the confluence of the glaciers to form the Firth of Clyde ice. The distribution of the more inland shells suggests their contemporaneity with the readvance of this paper. That they were deposited during a late and not an early period is borne out by the fact, emphasised many times by Mr. J. SMITH,† that the shells, like the Highland erratics, occur either in the upper boulder-clays or in the associated sands and gravels.

The highest limit of the marginal channels—*e.g.* in the Lammermuir and Moorfoot Hills, south of Muirkirk and east of Loch Ryan—is closely associated with this moraine. Since the greatest elevations in these different areas varies from about 1000 feet to only a few hundred feet above sea-level, and since, moreover, in certain areas local glaciers are entirely absent, it seems improbable that these marginal features represent the line of parting between the local glaciers and the Highland Ice, but rather the limit of a new advance.

The distributions sketched above, lying entirely within or north of these great moraines, suggests that at an earlier stage than the one under discussion the confluent ice-masses from the Highlands and Southern Uplands cleaved somewhere in the Central Valley, well north of the great moraine, the exact position being unknown and possibly undeterminable, and that following a retreat to north and south of uncertain extent a readvance occurred, during which the Highland Ice, except in the coastal areas, attained its farthest southern limit. Some of the more extensive of the interbedded sands and gravels, observed within or north of the moraine, may be shown by more detailed mapping than I have been able to make to be not merely the result of minor oscillations of the ice-edge but of an interstadial nature and origin.

Analogy with moraines of similar form and extent furnishes additional support for the view. The large kettle-moraines of North-west Europe and North America, especially those bounding the Newer Drift, have been generally, though not unanimously, regarded as indicating readvances which marked the close of retreats of interstadial or interglacial magnitude. A similar oscillation was postulated by the late Professor J. GEIKIE, and generally accepted, for the larger moraines of the Highlands of Scotland, while more recently a large movement of the ice-margin has been conclusively proved for the region of the Solway.‡

#### V. "NORTH-EAST IRELAND-ISLE OF MAN-CUMBERLAND MORaine."

A readvance of Scottish Ice along the north coast of Ireland, associated with an enormous moraine and formed after a period of retreat, has been postulated by Dr A. R. DWERRYHOUSE§ and the writer.|| A similar moraine has been the subject of prolonged study in the area around the head of Belfast Lough. It sets in in force near Holywood, skirts the Holywood Hills to Campbell College, swings into and across the Dundonald valley toward Dundonald, and continues along the lower slopes of the Castlereagh Hills by Rosetta, Newtonbreda,

\* *Irish Nat.*, xii (1903), p. 175.

† "Geology of Carlisle, Longtown, and Silloth District," *Mem. Geol. Survey* (1926), p. 47.

§ *Quart. Journ. Geol. Soc.*, lxxix (1923), p. 352.

+ *E.g.*, *Trans. Geol. Soc. Glasgow*, xi, Supplement (1898), p. 117.

|| *Proc. Roy. Irish Acad.*, xxxvi, Sect. B (1924), p. 294.

Edenderry, Ballyaghlis to the south of Lisburn, whence it curves across the Lagan valley to the foot of the basalt escarpment. Later crescentic moraines swing tangentially out of these lateral features, intersecting the median line of the valley in the neighbourhood of Lambeg, Dunmurry, and the Malone suburb of Belfast respectively.

These enormous accumulations of sands and gravels have previously been regarded\* as the delta of the River Lagan formed in a lake—"Lake Belfast"—ponded by the Scottish Ice standing down Belfast Lough. While the existence of such a lake at a slighter stage is indisputable, it seems difficult to believe that the River Lagan could produce a delta of this great surface extent and bulk. Such a reading of the evidence is in entire disagreement with the results of investigations made elsewhere, for it is a striking feature, constantly reinforced by repeated field observations, that normal drainage streams of the country, even where these are of considerable volume, were, in general, totally unable to form deltas other than quite diminutive features in extra-glacial lakes. Such deltas appear in Britain to be almost universally connected with the swollen torrents proceeding from the melting ice-edge, either directly, or indirectly as the overflows of glacial lakes.

A further difficulty in connection with the deltaic origin of the deposits of the River Lagan is the undoubted fact that the altitude of these so-called deltaic or lake deposits over large areas, especially along the margins of the valley, is considerably in excess of the height of the overflow which is supposed to have controlled the level of the lake waters.

That the material of the Belfast or Lagan moraines was derived from the ice, as is here contended, and not from land drainage, is confirmed by the not infrequent interdigitation and overriding of the sands and gravels by true boulder-clay, as is repeatedly stressed in the *Geological Memoir*,† by the considerable number of kettle-holes, and by the occurrence of well-marked esker ridges, at Lisburn and Dunmurry, which run within and transversely to the line of the great morainic accumulations. These eskers were merely incidents in the deposition of the moraines, formed as the Scottish Ice gradually retreated in a north-easterly direction down the valley of the Lagan. The so-called "Dundonald esker" is not a true esker, but is a residual ridge, transverse to the moraine, and carved out of it by the overflow waters of "Lake Belfast" at a slightly later period.

The land drainage held up at this period by the Scottish Ice in occupation of Belfast Lough and the lower part of the Bann, formed a greatly enlarged Lough Neagh, which drained by the valley at Pointzpass into Carlingford Lough.

The Lagan moraines, readily recognisable as far as Hollywood, become imperisistently and imperfectly formed to the east of this town, but can be traced discontinuously to the south of Bangor and of Donaghadee.

Along the east coast of Antrim these moraines have as yet been detected in only a few places; they span the wide valleys of Glenariff and Glendun. Though a systematic search of this country may be rewarded by their discovery, in other places it would seem that the steepness of the coast and the great modification and changes which have been post-glacially introduced by extensive landslipping would be unfavourable to their formation or preservation.

This great moraine of the coastal regions of the north-east of Ireland, so magnificently displayed where conditions were suitable, and exhibiting in its length, breadth, and form the characteristic features of the "Lammermuir-Stranraer Moraine," is separated from this moraine by the width of the North Channel. It is inconceivable that the one or the other, representing doubtless as they do considerable changes of climate of widespread distribution and

\* *Mem. Geol. Survey*, "Geology of the Country around Belfast" (1904), *c.g.* p. 63.  
† *Ibid.*, *c.g.* pp. 63, 75, 76, 98, 105, 106, 108, 113.



effect, could cease suddenly and without any trace of continuation. It is therefore tempting to correlate these two large moraines across the break, more especially as moraines of these dimensions are relatively rare. It seems more probable, however, that the North-east Ireland moraine corresponds with the large moraines of the Bride Hills\* of the northern plain of the Isle of Man, and with the readvance described from the Solway region of Cumberland,† and that the "Lammermuir-Stranraer Moraine" marks the edge of the ice at a later period, when it curved out to sea and possibly merely touched the Antrim coast. This correlation, rather than the other, is suggested, as it would seem improbable that the Scottish Ice, which was sufficiently powerful to attain the mouth of Lough Foyle and to penetrate the Lagan valley to the vicinity of Lisburn, would possess only strength sufficient to carry its edge on the Scottish side of the North Channel to Stranraer.

The more southerly latitude attained by the Scottish Ice in the west, as compared with the east, at the period of the "Lammermuir-Stranraer Moraine," is readily accounted for by the greater southerly extent of the Highlands in the west, by the advanced southerly position of the Arran Hills, with their powerful ice-radiation, and by the undisputed fact, borne out by numerous observations, that the greatest precipitation, at least in the later stages of the Glacial Period, lay in the west, giving rise to the more extensive and severe glaciation.

#### VI. LARGER CORRELATIONS.

The occurrence and distribution of the shelly drifts in the south-west of Scotland seem to throw light upon the conditions which obtained during the interstadial period of retreat. These marine shells may have been derived by the advancing ice from the bottom of the Firth of Clyde, either from near Greenock or from the wider part between Arran and Ayrshire. Yet if, as has been generally assumed, the source of the shells was the adjacent floor of the pre-glacial sea, it is strange, in view of the severe glaciation to which the area had been previously subjected (which might have been expected to remove effectually the bulk or all of this material) that the shells should be chiefly restricted to the latter clays and their associated sands and gravels, and should have such a relatively wide distribution. These considerations suggest that, during the interstadial interval preceding the readvance, the Clyde region was somewhat lower than to-day and that the sea had access to greater areas. The stratified layers with their Arctic marine shells, occurring in the drifts between Ayr and Mauchline and at an altitude of 250 to 300 feet above present sea-level,‡ may represent the interstadial deposits, as they appear to be too large in extent to have been materially displaced. Any such submergence was, however, strictly limited. There is no trace of it in the north of Ireland nor in the drifts of the lower ground of Galloway, which, as will be presently suggested, was ice-free at this period, nor again in the moraines of the east of Scotland. A partial depression of the region bearing the thickest ice-load merits no surprise, and is in strict accordance with events in Scandinavia and North America.

In connection with the distribution of the shelly drifts it may be observed that there are indications in Central Ayrshire of ice-flow from the west and south-west. Professor GREGORY§ concluded from an examination of glaciated surfaces near Lugton that ice proceeded north-easterly up the Lugton valley, a conclusion which seems difficult to reconcile with irrefutable evidence of glaciation from the north-east, later recorded|| from a rock-surface

\* *Mem. Geol. Survey*, "Geology of the Isle of Man" (1903), p. 431.

† *E.g.*, *Summary of Progress for 1922* (1923), p. 22; for 1924 (1925), p. 80.

‡ *Ibid.*, p. 78.

§ *Trans. Geol. Soc. Glasgow*, xiii (1906), p. 10.

|| *Summary of Progress for 1919* (1920), p. 30.

only some 20 yards away. It would seem, however, to be in agreement with evidence, in the shape of erratics of lava from the base of the New Red Sandstone, suggestive of a glacial carry from the west or south-west, obtained by Mr SIMPSON,\* and with the occurrence of boulders of Arran granite in the coastal part of Ayrshire, as noted by Mr J. SMITH† and confirmed during the course of these researches.

The "Lammermuir-Stranraer Moraine" was probably synchronous with the moraines of the "Kirkcowan Stage" of a previous paper. Though this correlation cannot, in the nature of things, be definitely established, the reasons which render it probable, though by no means certain, may be briefly stated.

Firstly, the absence of the moraine in South Ayrshire and the union of the ice-masses from the Highlands and Southern Uplands which this seems to entail, imply an extension to the south of the Galloway ice-axis, at least as far as the "Kirkcowan Stage," since a more or less symmetrical development of glaciers north and south of this axis is to be expected. Though this argument is not very strong, as any earlier stage with greater ice-extent would clearly satisfy the conditions, nevertheless it seems to exclude a later stage.

Secondly, the existence of the Stranraer portion of the moraine, with its outwash plain extending freely seaward, shows that the Galloway ice must at this period have lain with its western margin somewhere east of Luce Bay. Though this condition is met by all the "stages" described in the earlier paper, the later and smaller ones may be omitted for the reasons set out in the preceding paragraph.

Thirdly, the relatively high altitude of the snow-line at this time in the Pentland, Moorfoot, and Lammermuir Hills, as shown by the absence or very small extent of the local glaciation, would be in accordance with the height of the snow-line as worked out for the "Kirkcowan Stage" of the Galloway glaciation, provided due weight be given to the rise of the snow-line in an easterly direction.

Fourthly and less conclusively, the similar width, form, and conspicuousness of the moraines lend support to the suggested correlation.

Should this correlation prove correct, additional weight would be added to the arguments already given in favour of the readvance origin of the "Lammermuir-Stranraer Moraine," as the Kirkcowan moraines have been shown to be indicative of a large oscillation.

The sharp delimitation of the moraines at Kaimrig End and west of the Lochurds Hills (p. 30), together with the free escape of the melt-waters from the ice-edge southward into the Biggar Water, would appear to prove that the Tweed valley below its confluence with this stream was ice-free at this period, and that the glaciers, fed by the snows on Culter Fell and the hills south of Peebles, and streaming down the valleys of the upper Tweed, Yarrow, and the Ettrick Water, were confined within these valleys. This would also seem to have been the state of affairs when, at a slightly later stage, the broad and flat-floored valley of the Biggar Gap served as the means of escape for the surplus waters of the great "Lake Clyde," which was impounded by the Highland Ice in occupation of the Clyde valley during its stepwise retreat northward from the region of Lanark and Carstairs.

It is not proposed to discuss here the evolution of the Southern Upland rivers, nor the history of the Clyde-Tweed drainage and the initiation of the Biggar Gap. That the Clyde originally drained into the Tweed by this gap was suggested by Sir A. GEIKIE,‡ later developed by Sir H. J. MACKINDER,§ and accepted by Professor J. W. GREGORY.¶ That story is

\* Cf. *Summary of Progress for 1921 (1922)*, p. 78.

† *Scenery of Scotland*, 3rd ed. (1901), p. 378.

‡ *Trans. Geol. Soc. Glasgow*, xv (1916), p. 301.

§ *Brit. Assoc. Handbook, Glasgow* (1901), p. 524.

¶ *Britain and the British Seas* (1902), p. 132.



one of considerable antiquity, and is long pre-glacial. It is here contended that the drainage from west to east also took place for a considerable time during the later phases of the Glacial Period, when glacial "Lake Clyde" discharged by this gap. By this exit the melt-waters from the snout of the receding Upper Clyde Glacier, from the many miles of the margin of the Highland Ice standing below Lanark, and the land drainage from the ice-free country about the Hagshaw Hills and the Douglas basin found escape.

That the Tweed below the confluence with the Biggar Water should be ice-free at the time when the Galloway Hills were severely glaciated, as is here maintained, seems surprising, in view of the altitude of the mountains in which this river rises. Yet the contrast of the Pentland, Moorfoot, and Lammermuir Hills with the Galloway Hills at the same stage, the undoubted rise of the glacial snow-line eastward at this period, the fact that the mass of high ground between Nithdale and the North Channel was the chief seat of the glaciers in the south of Scotland,\* together with the behaviour of the drainage and of the moraines as set out above, appear to lead to no other conclusion.

The moraines of Duns, north of Greenlaw, Eckford, Morebattle, Wark, Cornhill, and of Jedburgh and Galashiels in the Tweed basin, would seem to belong to an earlier phase, and may, perhaps, be correlated with the "North-east Ireland-Isle of Man-Cumberland Moraine."

If, as is here submitted, the corrie glaciers of the Lammermuirs and the valley glaciers of upper Tweeddale, Yarrow, and Ettrick Water were contemporaneous with the "Kirkeowan Stage" of the Galloway glaciation and with the "Lammermuir-Stranraer Moraine" of the Highland Ice, then it would follow that the correlation of the moraines of the valleys of the Highlands of Scotland with similar ones in the Southern Uplands and in other mountains of Britain, maintained by the late Professor J. GEIKIE † and generally held, is no longer tenable.

The "North-east Ireland-Isle of Man-Cumberland Moraine" is tentatively linked up with the Baltic moraine of North Germany; the "Lammermuir-Stranraer Moraine," the "Pentland-Maybole Moraine," and the later moraines of this paper, together with those of the "Moraine Glaciation" of the Highlands of Scotland, then fall naturally into the position of British representatives of the Ra and other moraines of Scandinavia, and the "post-glacial" stages of Penck and Brückner, established for the Alps.

## VII. SUMMARY OF CONCLUSIONS.

A well-marked kame-moraine, the "Lammermuir-Stranraer Moraine," margining the Central Valley on the south, has been traced from the east coast, south of St Abb's Head, along the northern slopes of the Lammermuir and Moorfoot Hills to the Clyde above Lanark, and by Muirkirk to the hills near New Cumnock, occurring again, after a break in south Ayrshire, at Stranraer and in the Rhinns of Galloway. The ice-sheet at this stage was still extremely powerful. It filled the Central Valley, overrode the Pentland Hills, abutted against the northern flanks of the Southern Uplands to an altitude exceeding 1000 feet above sea-level, excluded the shallow seas on the west, and spread to an indeterminate distance over the floor of the North Sea on the east.

Consequent upon the melting and thinning of the ice, the highest summits of the Pentland Hills appeared as nunataks; further melting enlarged these nunataks, causing a shadow area of low ice-pressure and finally an entirely ice-free zone, about Penicuik, to arise in the lee. Out of the corridor, therefore, south of the Pentlands, the ice withdrew as two lobes—the "Esk Lobe" to the north and north-east, the "Dolphinton Lobe" to the west. Moraines and

\* Sir A. GEIKIE, *Scenery of Scotland*, 3rd ed. (1901), p. 347.

† *E.g.*, *Scot. Geog. Mag.*, viii (1892), map opposite p. 362.

marginal channels mark the successive stages of the retreat. Simultaneously, the ice fell back from the Lammermuirs; Professor KENDALL and Mr BAILEY have indicated the mode of recession.

At the maximum extent, the Highland Ice was confluent with the Upper Clydesdale Glacier about Symington and Biggar and with the Tinto Glacier. Progressive melting broke up this ice into its three components; the great numbers of moraines above Lanark show the manner and phases of the separation and retreat.

The thinning of the ice north of Muirkirk led to the early emergence of the Hagshaw and Nutberry Hills and the formation of two lobes—the one thrust westward into the Douglas Water from the west, the other over the area of Airds Moss and the upper Ayr from the west.

The “Lammermuir-Stranraer Moraine” is entirely absent from the hillsides between New Cumnock and Loch Ryan. This important break implies the confluence at this period of the Northern Ice with the glaciers centred in the western part of the Southern Uplands.

The free ice-margin with its moraines was discovered at Stranraer, encircling the head of Loch Ryan and passing to the west coast of the Rhinns of Galloway.

A later line, represented by an equally well-developed moraine—the “Pentland-Maybole Moraine”—and associated with marginal drainage features, is traceable across the Esk valley, along the north slopes of the Pentland Hills to Carstairs, and along the south sides of the Avon and Irvine to near Galston, reappearing after a break, indicating the union of the Highland Ice with the Doon and Lugar Water Glaciers of the Southern Uplands, in the valley of the Girvan Water, *e.g.* at Maybole, and along the Ayrshire coast, *e.g.* at Culzean, whence the ice-front curved out to sea.

Following this stage, the ice broke up into the Forth and Clyde Glaciers, the edge of the one retreating northward to its lateral moraine—the Polmont kame—the other receding westward from the upland north-east of Lanark. Moraines and marginal channels mark the retreat of the Clyde Glacier down the Clyde toward Glasgow and the withdrawal of the lobes thrust from the edge of this glacier into the valleys of the Avon and Bonny Water.

The surplus waters of glacial “Lake Clyde,” so impounded, escaped by the Biggar Gap into the Tweed, which was ice-free.

At the period of the “Lammermuir-Stranraer Moraine” small corrie glaciers only existed in the Lammermuir Hills, valley glaciers occupied the larger valleys of the hills south of Peebles—the Tweed below the confluence with the Biggar Water was ice-free—while the ice in the western part of the Southern Uplands was at its “Kirkcowan Stage” of development.

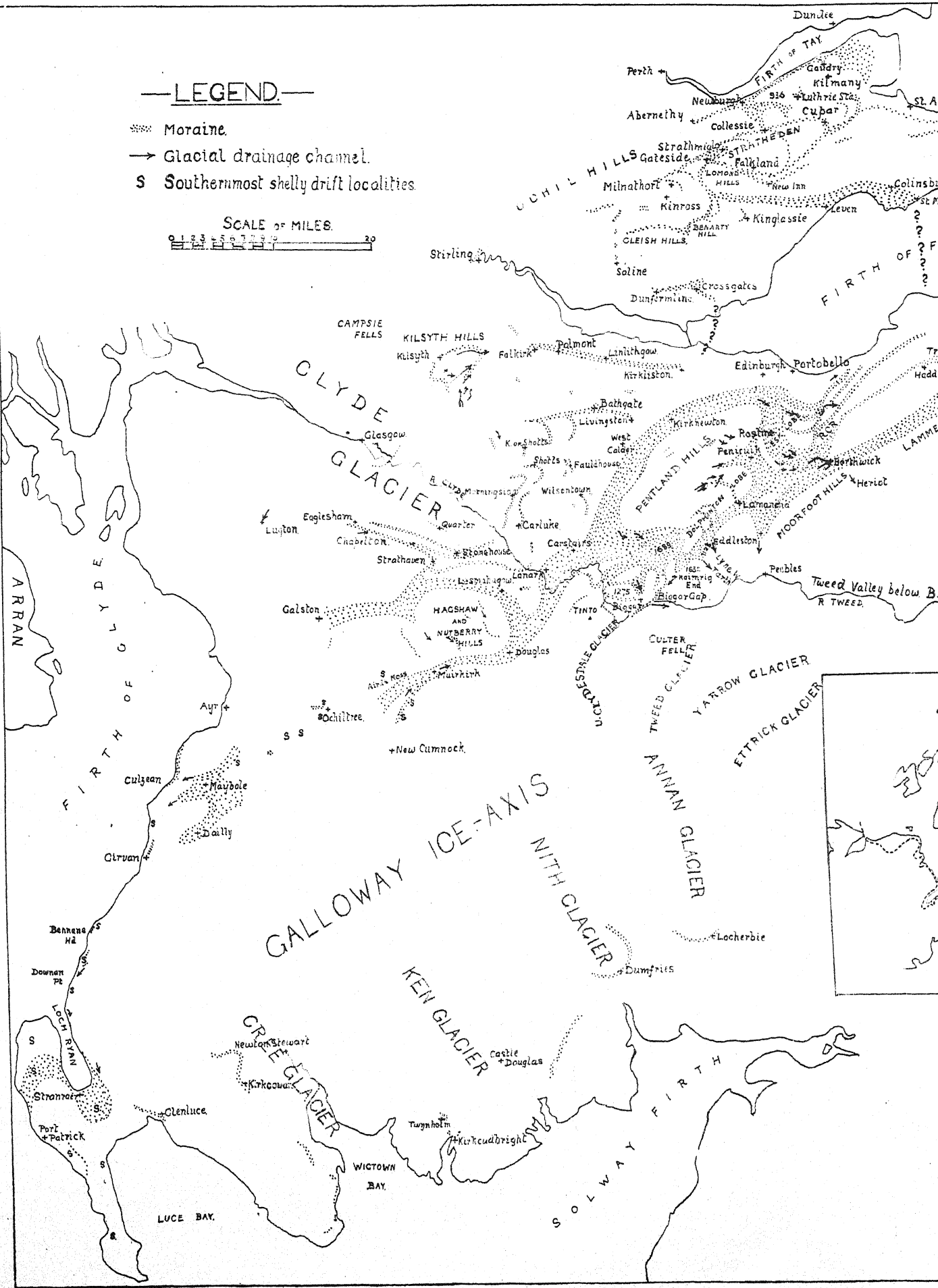
The “North-east Ireland-Isle of Man-Cumberland Moraine” of this paper is correlated with the Baltic moraine of North Germany; the “Lammermuir-Stranraer Moraine,” the “Pentland-Maybole Moraine,” the later moraines, including the “Moraine Glaciation” of the Highlands of Scotland, are correlated with the Ra and other moraines of Scandinavia and the “post-glacial” stages of the Alps.

#### EXPLANATION OF MAP.

A map of the south of Scotland showing the position of the kame-moraines; R.C.R. = Roman Camp Ridge; 1869 = Black Mount; 1632 = Lochurds Hills; 1275 = hill N.W. of Biggar; lines of interrogation marks give the suggested positions of the snout of the Forth Glacier at two important stages. In Galloway are shown the moraines of the “Kirkcowan Stage.”

Inset.—Map showing the position of the ice-edge at three stages. Dash line = “North-east Ireland-Isle of Man-Cumberland Moraine”; dot and dash line, the “Lammermuir-Stranraer Moraine” and its Southern Upland equivalent; the dotted line, the “Pentland-Maybole Moraine.”





MAP SHOWING SUCCESSIVE POSITIONS OF THE ICE FRONT IN THE CENTRAL

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III.—The Petrology of Iceland. By G. W. Tyrrell, A.R.C.Sc., Ph.D., F.G.S., Lecturer in Geology, University, Glasgow, and Martin A. Peacock, B.Sc., Ph.D., Carnegie Research Fellow, University, Glasgow. (With Two Plates and Four Text-figures.)

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PREFACE.

Kainozoic eruptives, preponderantly of basaltic composition, occupy parts of Scotland, Ireland, Greenland, Spitsbergen, and King Charles Land, the major part of Franz Josef Land, and the entirety of Iceland, the Faeroes, and Jan Mayen. These regions have been

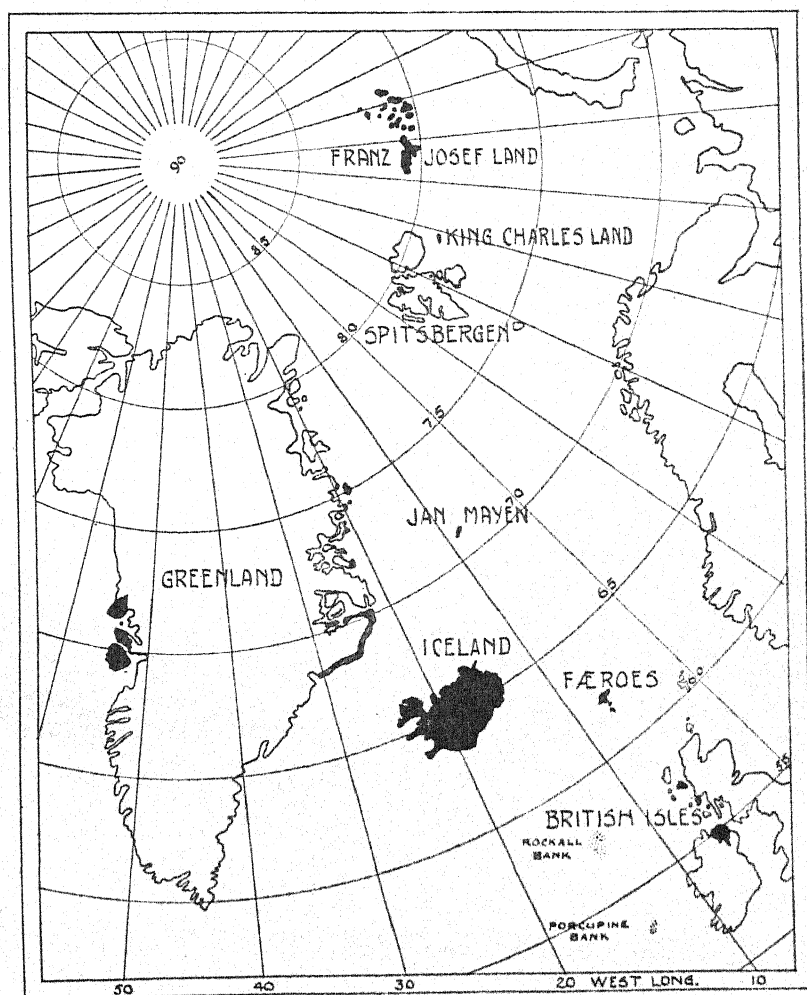


FIG. 1.—Sketch-map of the Thulean or Brito-Arctic Petrographic Province. The areas in black are occupied by Kainozoic eruptives. Rockall Bank and Porcupine Bank, from which dredged blocks are chiefly basaltic, have been included.

grouped together as the Thulean or Brito-Arctic Petrographic Province (fig. 1); they represent the relics of an extensive basaltic plateau-land, the greater part of which foundered beneath the North Atlantic and Arctic Oceans in late Kainozoic times. By virtue of its size, central position, diversity, and accessibility, Iceland is perhaps the most instructive region in the whole province. The interest in that country is heightened,

furthermore, by the fact that whereas in all the other regions mentioned, with the exception of Jan Mayen, volcanicity expired before the advent of the Pleistocene and did not recur, Iceland became the theatre of a vigorous resumption of igneous activity which took place in Early-glacial times, and has continued uninterruptedly to the present day.

Although a number of important contributions to the petrography and petrology of Iceland have appeared in recent years,\* the petrographic character of this region and its relations to the Thulean Province are yet insufficiently understood. With a view to collecting material for a more comprehensive study of the Icelandic eruptives, the authors visited Iceland in the summer of 1924. In the course of an itinerary which embraced the country lying between the Torfajökull in the south and the Hvammsfjörður in the north-west some four hundred rock-specimens were collected. On the return journey from Reykjavík to Leith specimens were collected at the various northern and eastern ports of call. The material thus obtained forms the basis of the present and the ensuing studies.

For the better understanding of the mutual relations of the various rock-groups which will be treated as petrographic units, a brief summary of the geological succession in Iceland will be given. Such a summary may best be illustrated by a schematic section stretching from Glettinganes in the extreme east, through the Tindfjallajökull in the south, and continuing to the Patreksfjörður in the north-west peninsula (fig. 2).

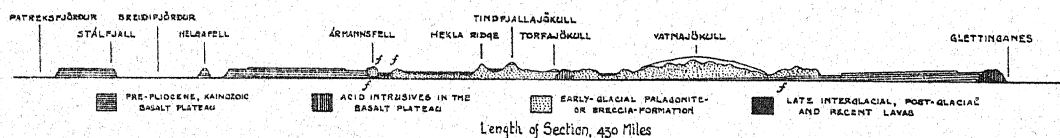


FIG. 2.—Schematic section across Iceland from Glettinganes in the extreme east, through the Tindfjallajökull in the south, to the Patreksfjörður in the north-west peninsula. The ice-sheets are shown blank.

In Iceland we may distinguish three formations which are distinct both in petrographic character and in age. These are:

3. The Recent, Post-glacial, and Late-interglacial eruptives.
2. The Early-glacial Breccia or Palagonite Formation.
1. The pre-Pliocene Kainozoic Basalt Plateau.

Formations 1 and 2 are separated by a period of volcanic rest in the Pliocene, during which time Crag sediments were deposited. A tectonic phase, which is well defined in the south of Iceland, separates Formations 2 and 3.

The pre-Pliocene Kainozoic Basalt Plateau was derived from sources which were probably outwith the present Iceland. It contains plant-beds which have been referred to the Miocene, acid and basic intrusives, and thin, red, interbasaltic tuff-partings. The old plateau is exposed in the east and in the west of Iceland; centrally it has sunk in and has been covered by younger formations. With the advent of the Glacial Period volcanic energy, which had lain moribund during the Pliocene, broke out with renewed vigour, building up the Breccia- or Palagonite-Formation which in thickness and extent probably outrivals the older basalt plateau. The Breccia Formation consists of tuffs and breccias associated with basic intrusions which frequently have globular structure, moraines, boulder-clays, and glacial sediments. Following a period of faulting and subsidence, ameliorating glacial conditions accompanied a reversion to dominant lava-production. This phase is represented by the Late-interglacial, Post-glacial, and Recent eruptives, which, although chiefly basaltic, have acid representatives. In the highlands the relics of the

\* Lists of literature will be given later.



Pleistocene Ice-sheet lingered on, and sub-glacial volcanoes continued to produce tuffs and breccias.

In arranging the petrographic material for description and discussion, it was decided to adopt the following grouping: the basalts of the pre-Pliocene Kainozoic Plateau; the acid intrusives in the Basalt Plateau; the basic tuffs; and the Late-interglacial, Post-glacial, and Recent basaltic eruptives. It is intended that these four groups shall form the subjects of separate papers embodying the independent studies of one or other of the authors. The final general discussion, in which the relations of the Icelandic area to the Thulean Province will be treated, will be undertaken jointly. As chronological order need not necessarily be preserved, the order of appearance of the papers dealing with the four rock-groups will be determined by expediency. The basic tuffs have been selected for first treatment, as one of us has already gained some specialised experience in the interpretation of these rather remarkable rocks.

## PART I.—THE BASIC TUFFS, by MARTIN A. PEACOCK.

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### I. INTRODUCTION.

#### 1. *Scope of the Present Paper.*

As was indicated in the Preface, basic tuffs, in the form of thin red partings, represent a subordinate component of the Basalt Plateau. As the few specimens which were collected from these pre-Pliocene tuff-bands present no features which have not already been described,\* these rocks do not call for further treatment. Basic tuffs are, however, the main constituent of the Early-glacial Breccia Formation, and they are the chief products of younger eruptions under and around the present ice-fields. Specimens of the finer-grained facies of the Glacial and later tuffs thus form the subject of the present study. As the classic Icelandic examples of palagonite-tuff occur in the Breccia Formation, and as the nature and origin of palagonite are most imperfectly understood, this study will of necessity develop into an attack on the palagonite question.

#### 2. *Review of Previous Work.*

The Breccia Formation of Iceland, with its arresting scenery, imposing massiveness and bewildering heterogeneity, and the remarkable alteration displayed by certain of its

\* HAWKES, 1916; Author, 1924-5 (B), pp. 316-18, pl. iv, fig. 10.

constituents, has attracted the attention of a number of geologists, and has given rise to the expression of divers views regarding its age, origin, constitution, and partial alteration. The greater bulk of previous work has been directed to the elucidation of questions of age and origin; records of microscopical and chemical studies are few, and the conclusions which they contain are divergent.

The first important work is that of SARTORIUS VON WALTERSHAUSEN, who visited Iceland in company with BUNSEN in 1846. During this visit VON WALTERSHAUSEN first observed in the tuffs of the Breccia Formation the widespread occurrence and pure development of a substance which he had already noticed in the matrix of a tuff from Aci Castello, Sicily, in 1837, and to which, from its wider distribution in the shell-bearing tuffs of Palagonia in the Val di Noto in Sicily, he gave the name *Palagonit* in 1847.\* VON WALTERSHAUSEN described palagonite as "a fully transparent wine-yellow to resin-brown mineral of vitreous lustre and hackly conchoidal fracture, the external appearance of the substance being very similar to that of gum-arabic or brown sugar. Its hardness scarcely exceeds that of calcite, and its specific gravity is close to 2.64."† Besides forming an important component of the Icelandic tuffs, palagonite was found in the exceptional occurrence at Seljadalur, near Reykjavik, to constitute an apparently homogeneous bed 50 feet in thickness. This occurrence was described as *Palagonitfels*, and VON WALTERSHAUSEN observed that the rock might be confused by the untrained eye with certain types of pitchstone. VON WALTERSHAUSEN's theory to explain the origin of this rock was the same as the one which he formulated for the Sicilian occurrence, namely, that "the finely powdered volcanic ashes of submarine eruptions fell back into the sea and were cemented into a kind of hydraulic mortar, part of which thereby acquired a fixed chemical constitution, while the other part, enveloped by this material, remained in its original condition."‡

In a later work§ VON WALTERSHAUSEN summarised his views on palagonite. On account of the variations in the chemical composition of different samples, he regarded palagonite as a mineral group, each member of which consisted of a mixture of ideal mineralogically inseparable "orthotype" and "heterotype" palagonites; to these ideal types he gave chemical formulæ which contained  $H_2O$  as essential and variable components. In addition to these hydrous palagonites VON WALTERSHAUSEN observed that the Icelandic tuffs contained an anhydrous, black substance of pitch-like lustre, to which he gave the name *Sideromelan*. This material was recognised as a mineral species whose chemical constitution was such that the addition of three molecules of water to it produced an orthotype palagonite.

BUNSEN made careful analyses of some of the specimens collected during his joint visit to Iceland with VON WALTERSHAUSEN. He showed that palagonite, except for the large and variable water content, agreed in composition with the "normal basalt magma."|| He further demonstrated that a palagonitic substance, agreeing mineralogically and chemically with the Icelandic palagonite, could be obtained by treating basalt powder with fused caustic potash and leaching out the soluble products.¶ To account for the formation of palagonite in nature BUNSEN postulated, in addition to the "normal-pyroxenitic" and "normal-trachytic" magmas, a third, now extinct, magma source which delivered alkali-rich silicates. He believed that palagonite was produced, as in the laboratory, by the

\* 1847, pp. 394 *et seq.*, and footnote 1.

† PENCK, 1879, p. 504 (trans.).

‡ VON WALTERSHAUSEN, *op. cit.*, p. 400 (trans.).

§ "Ueber die vulkanischen Gesteine von Island und Sicilien" (*n.s.*); the above information is derived from PENCK, *op. cit.*

|| "Normal-pyroxenische Mischung."

¶ 1851, p. 856.



action of water at high temperatures on these alkali-rich silicates.\* In an earlier work BUNSEN already made the significant observation that the hot springs of Iceland appeared to be most intimately connected with the breccia mountains.†

The above investigations of the palagonite-tuffs contain no reference to microscopic work, and hence no criteria by which palagonite might be recognised in thin sections. Microscopical studies soon showed that even the purest *Palagonitfels* did not consist of a single homogeneous substance which might be called palagonite. The following statement by ROSENBUSCH expresses the general conclusions of several investigations following the work of BUNSEN: "... it appears that the palagonite substance is not homogeneous, and that analyses of palagonite are bulk analyses of basalt glass together with its alteration products and separated minerals."‡

In 1879 PENCK published a thorough review of the whole subject. After an extended re-examination of specimens of *Palagonitfels* and palagonite-tuff from Iceland and Sicily, and a study of tuffs reported as palagonitic from various other localities, PENCK arrived at the following conclusion: "Es darf daher gerechtfertigt sein anzunehmen, dass ein als Palagonit zu bezeichnender Körper nicht existiert." . . . § This authoritative judgment dealt the final blow to palagonite, and the term became degraded from the rank of a mineral species to be a general designation for any hydrous, altered, basaltic glass.||

In the course of two recent papers¶ the present writer touched on some aspects of the palagonite question. In the first paper, in which MACKENZIE's collection of Icelandic rocks was described,\*\* it was observed that palagonitisation was a hydration process which attacked translucent basalt glasses. Three stages in the process were distinguished: (1) a bleaching of the margins of the fresh vitreous fragments; (2) the passage of the bleached margins into a fibrous mineral which is rich in water and in ferric oxide, poor in lime, and poor in, or free from, alkalies; (3) the formation of calcite and zeolites representing the fixation of the lime and the alkalies released in the second stage. The third stage was not represented when the liberated lime and alkalies were carried away by permeating solutions.†† None of these products was definitely identified with the palagonite of VON WALTERSHAUSEN.

In the second paper a palagonite-tuff from Viðey was considered in some detail. It was found that the fresh, translucent glass fragments which had suffered marginal palagonitisation were negligibly vesicular and possessed an initial water content of about 4 per cent.; they were therefore named "hydrotachylyte."‡‡ As the Viðey palagonite-tuffs must have been originally hydrotachylyte-tuffs, and as they were associated with basalts of globular structure, and as, furthermore, similar occurrences of palagonite-tuff and globular basalt were found associated with glacial sediments in other localities in Iceland, it was concluded that the Viðey hydrotachylyte-tuffs and the underlying globular basalts had originated from a series of restrained "Sub-glacial extrusions."§§

Although it is certain that the substance which VON WALTERSHAUSEN named palagonite does not conform to the accepted criteria of a mineral species or a mineral group, and that the rock which he called *Palagonitfels* is not composed of a single, homogeneous material which might be called palagonite, it is equally certain that palagonitisation, i.e. the alteration which rocks described as palagonitic have manifestly suffered is a definite

\* *Op. cit.*, p. 279.

† 1847, p. 279.

‡ 1908, p. 1317 (trans.).

§ 1879, p. 568.

|| As defined by HOLMES, 1921.

¶ Author, 1924-5 (B), pp. 308-15; *idem*, 1926.

\*\* For an account of MACKENZIE's visit to Iceland in 1810, see the Author, 1924-5 (A).

†† 1924-5 (B), p. 313.

‡‡ 1926, p. 455.

§§ *Ibid.*, pp. 462-3.

process characteristic of the tuffs of Iceland, and of rocks from at least two other regions. If it can be shown that the palagonite-tuffs are characterised by the presence of an alteration substance for which no other petrographic name is available, and which at the same time imparts to the tuffs the various characters which were ascribed to *Palagonit* by VON WALTERSHAUSEN, we shall be justified in naming that material palagonite. In the following descriptions it will emerge that such a substance does exist.

The specimens described are a few typical ones arranged in the order calculated best to illustrate the progress of palagonitisation. The non-palagonitic tuffs consist essentially of VON WALTERSHAUSEN's *Sideromelan*, while the palagonite-tuffs are all altered sideromelan-tuffs. The following classification has therefore been adopted: (1) sideromelan-tuff; (2) palagonitic tuff, in which sideromelan shows incipient alteration; (3) palagonite-tuff, in which the alteration is considerable; and (4) palagonite-rock, in which the alteration is so advanced that the rock has all the properties which were ascribed to *Palagonitfels* by VON WALTERSHAUSEN.

## II. PETROGRAPHY.

### 1. *Sideromelan-Tuff*.

A typical sideromelan-tuff will be considered in some detail, as it consists very largely of the material which subsequent examples will show to be the invariable parent substance of palagonite.

*Occurrence*.—A specimen of this type (T 21) was found overlying a series of palagonite-tuffs, intrusive basalts with globular structure, and glacial sediments, and overlain by Late-interglacial doleritic lavas in the W. wall of the gorge of the Hvítá at Gullfoss.\*

*Hand-specimen*.—This consists of cuboidal fragments of dense, non-lustrous basalt glass cemented by a scanty, brownish-white, argillaceous matrix. These fragments grade in size from 1 cub. cm. downwards; their bounding surfaces are sometimes conchoidal.

*Microstudy*.—In thin section (Pl. I, fig. 1) the glass constituting the vitreous fragments is seen to be of the palest apple-green colour, perfectly fresh, transparent, and non-vesicular. It is traversed by an irregular network of cracks, and the boundaries of the separate fragments are determined by similar fracture lines. The refractive index of the glass is 1.607.† The glass contains microlites of olivine and plagioclase whose dimensions are usually less than the thickness of the slice. The olivine, which occupies 4 per cent. of the glassy fragments by volume,‡ occurs as isolated, rounded crystals and crystal-aggregates of the common variety whose refractive index reaches a maximum of 1.699 (LARSEN). The feldspar, whose volume proportion is 5 per cent., appears in euhedral tablets, many of which are completely surrounded by the glass and are clearly visible only in polarised light. With multiple twinning and a maximum refractive index of 1.590, the feldspar is pure anorthite.

The scanty argillaceous matrix which binds these fragments makes sharp boundaries with the fresh glass and does not appear to be an alteration product of the latter. It is

\* For a fuller description of this section, see the Author, 1926, p. 453, and fig. 8.

† The refractive index measurements recorded in this paper were made by the immersion method using a lately recalibrated series of thirty-eight liquids, grading in steps of 0.010 from 1.400 to 1.770. By mixing drops from adjacent bottles, steps of 0.005 were obtained, while the digit in the third place was obtained by estimating the relative strengths of the Becke effect in two liquids, thus differing by 0.005. The measurements may be regarded as liable to an error not exceeding  $\pm 0.002$ .

‡ Volume percentages were obtained by means of a microcamera in which the ground-glass screen was replaced by a plate of clear glass covered with thin squared paper. The outlines of the constituents were traced in partial darkness, and their proportions were estimated by counting squares. A 4-inch circle was used with paper squared in  $\frac{1}{16}$ ths of an inch.



brown in various shades, shows dull aggregate polarisation which approaches isotropism, and has the appearance of being somewhat porcellanised.

*Chemical Composition.*—With the small and approximately equal separation of felsic and mafic microlites, the composition of the pure glass cannot differ notably from the aggregate composition of the glass with its microlitic content. Fragments of the latter were therefore selected, freed from matrix, and analysed. For comparison the result is tabulated together with an analysis of sideromelan from the palagonite core of a manganese nodule from the South Pacific, and an analysis of the Late-interglacial doleritic lava of Reykjavik, Iceland.

	I.	II.	III.
SiO <sub>2</sub>	46.39	46.84	48.06
Al <sub>2</sub> O <sub>3</sub>	16.27	17.78	12.14
Fe <sub>2</sub> O <sub>3</sub>	1.35	1.64	4.89
FeO	9.96	10.79	9.04
MgO	9.77	9.24	9.80
CaO	13.00	11.87	12.23
Na <sub>2</sub> O	1.40	2.02	2.07
K <sub>2</sub> O	0.15	0.28	0.31
H <sub>2</sub> O +	0.15	n.d.	0.10
H <sub>2</sub> O -	0.10	n.d.	0.04
TiO <sub>2</sub>	1.27	n.d.	1.55
P <sub>2</sub> O <sub>5</sub>	0.05	n.d.	0.07
MnO	trace	0.34	0.17
CO <sub>2</sub>	none	n.d.	none
S	none	n.d.	0.01
	99.86	100.80	100.48 *

I. Sideromelan. Gullfoss, Iceland. Analyst, W. H. and F. HERDSMAN.

II. Basic Volcanic Glass (Sideromelan). Station 302, lat. 42° 43' S., long. 82° 11' W., 1450 fathoms. Analyst, RENARD. MURRAY and RENARD, 1891, p. 464.

III. "Pre-Glacial" (actually Late-interglacial) Basalt. Reykjavik, Iceland. Analyst, WASHINGTON. WASHINGTON, 1922, p. 783.

The theoretical mineral constitution derived from the new analysis is:

Albite	12.05
Anorthite	38.09
Diopside	21.48
Hypersthene	8.70
Olivine	14.77
Magnetite	2.09
Ilmenite	2.43
Water, etc.	0.45
	100.06

\* Including: ZrO<sub>2</sub>, none; Cr<sub>2</sub>O<sub>3</sub>, none; BaO, none.

while the following are the positions of the analyses in the Quantitative Classification:—

I.	III.	5.	4(5).	5.
II.	" III.	5.	4.	" 5.
III.	III."	5.	4.	" 5.

The analysis, refractive index, and microlitic content of the Gullfoss sideromelan, all indicate a rather basic, basaltic composition. The norm shows that the rock is sufficiently undersaturated with respect to silica to form 15 per cent. of olivine. The low alkalis of the analysis, especially the negligible potash, result in bytownite, practically free from the orthoclase molecule, as the theoretical plagioclase; the modal plagioclase, anorthite, reflects the invariably more calcic character of early-formed plagioclases.

Comparing firstly analyses I and II, it will be seen, despite the inferior quality of RENARD'S analysis as judged by modern standards, that the agreement in all essentials is remarkably good. From the high summation of the analysis of the deep-sea example, it may be inferred that  $H_2O$ , which was not determined, is negligibly small and thus comparable to the value in the Icelandic specimen. This striking agreement between I and II is not, however, to be regarded as indicating a constancy in the chemical composition of sideromelan. While still preserving the mineralogical characters of sideromelan, namely translucency and freedom from separated ores, the Sicilian sideromelan has a much more alkalic composition.\*

The general agreement between I and III supports the field evidence which indicated that the Gullfoss sideromelan-tuff was derived from the same magma which produced the Late-interglacial doleritic lavas. The change from tuff-production to lava-production undoubtedly corresponded with the Interglacial recession of the ice-sheet from the Gullfoss district.

The second example of sideromelan-tuff is characterised by a ferruginous cement.

*Occurrence.*—Another example of sideromelan-tuff (T 106) was collected at 2100 feet from the Hungurskarð, the breccia foot-hills lying 1 mile N. of the present northern limit of the ice on the Tindfjallajökull. The tuff serves to bind together large and small basalt-masses. The smaller of these are angular and vesicular, while the larger basaltic inclusions exhibit the same globular structure which was observed at Gullfoss.†

*Hand-specimen.*—This is a uniformly fine-grained, compact, red-brown tuff containing vesicular basalt fragments. The unaided eye can distinguish black, vitreous specks in a red-brown matrix.

*Microstudy.*—The thin section (Pl. I, fig. 2) is composed of typical sideromelan fragments cemented by a ferruginous matrix. These fragments have an average grain-size of 0.4 mm., and a refractive index of 1.612; in every other microscopic character they accord with the sideromelan of T 21. The cementing material is structureless, and varies in colour from deep red to almost black. It is faintly anisotropic, the true polarisation colours being masked, however, by the strong, blood-red absorption. As the refractive index of the red material is variable, lying both above and below 1.77, and much lower than that of hæmatite, limonite, or goethite, it cannot be identified with these minerals. The appearance of the section and of small fragments in temporary mounts suggests that the red material is essentially sideromelan which has absorbed travelling colloidal solutions of iron, thereby becoming deeply stained. The faint double refraction and variable

\* WASHINGTON, 1917, pp. 696-7.

† Page 56, and footnote.



refractive index of the red material may be ascribed to incipient crystallisation of definite iron compounds following dehydration.

The last example of sideromelan-tuff is characterised by a zeolitic cement.

*Occurrence.*—This rock was obtained near sea-level from the matrix of the agglomerate on the S. side of the Béjarfell, Reykjanes (R 21).\* As in the case of the Gullfoss examples, this rock is associated with palagonite-tuffs and globular basalts.

*Hand-specimen.*—The rock is a friable aggregate of minute, black particles of glass which are cemented by a subordinate amount of greyish-white material. The vitreous fragments exceptionally reach 2 mm. in their greatest dimensions, and occasionally they may be seen to hold small felspar microlites.

*Microstudy.*—The thin section (Pl. I, fig. 3) consists of sideromelan fragments cemented by zeolitic films. These glassy fragments have a refractive index of 1.604. Except on their extreme margins, they are perfectly fresh, homogeneous, translucent, and pale grey-brown in colour. The fragments are somewhat vesicular, and their boundaries are defined by curved cracks which have often traversed the zones of weakness between adjacent steam cavities, producing typical ash-structures. In the larger fragments are found occasional glomero-porphyritic aggregates of fresh, euhedral bytownite tablets whose maximum refractive index is 1.582.

The extreme margin of each sideromelan fragment is marked by a continuous, narrow, dark alteration-selvedge which preserves a uniform width of 0.01 mm. Many of the totally enclosed steam cavities are provided with similar linings; when these linings are absent they have apparently been removed in grinding. The alteration-selvedges are composite, consisting, as we pass outwards from the fresh glass, of a narrower dark band about 0.01 mm. wide, and a broader colourless band which is about 0.02 mm. in width. With the  $\frac{1}{2}$ -inch objective the dark bands resolve into zones of minute, opaque globulites whose formation has slightly bleached the intervening glass. These globulites cannot be determined, but it may be surmised that they represent part of the iron content of the altered margins. The colourless bands are composed of zeolites. Between crossed nicols they are seen to consist of minute, faintly birefracting fibres which lie normal to the extension of the selvedges. When two such fibrous selvedges meet, the wedge-shaped interspace is sometimes filled with a non-fibrous, isotropic zeolite. Examined in small fragments immersed in standardised media, the isotropic zeolite was found to have a refractive index very slightly below 1.480, thus definitely ruling out analcite ( $n=1.487$ , LARSEN). The only isotropic zeolite with a refractive index lower than that of analcite is faujasite ( $n=1.48$ , LARSEN), with which the mineral in question is therefore identified. The fibrous zeolite gives straight extinction and has very low birefringence; its measured refractive index range is from slightly below 1.480 to distinctly above 1.470. The mineral is therefore identified with ptilolite ( $\alpha=1.476$ ,  $\beta=1.48$ ,  $\gamma=1.480$ , LARSEN). Although zeolites, as will be seen later, are end-products in the hydration of sideromelan, the absence of other signs of alteration in this rock indicates that the zeolitic films described have not been derived from the sideromelan margins to which they are attached, and have therefore been precipitated from travelling solutions.

*Water Content.*—A sample of this rock yielded the following results:—

H <sub>2</sub> O at 105°	0.90 per cent.
H <sub>2</sub> O above 105°	0.97 "
	1.87 "

\* For a fuller account of the breccia inlier at Reykjanes, see the Author, 1926, pp. 451-2, and fig. 6.

As the zeolitic films must contain some of this water, it may be concluded that the fresh sideromelan, as in the case of the fully analysed example (T 21), is practically anhydrous.

## 2. *Palagonitic Tuff.*

*Occurrence.*—A specimen illustrating the early stages of palagonitisation (S 115c) was collected from the Búrfell,  $3\frac{1}{2}$  miles S.S.E. of Sandur on the Snæfells Peninsula. The Búrfell is an isolated breccia-hill 720 feet in height; its flanks rise steeply from the 300-foot lava-covered platform which surrounds the Snæfellsjökull.

*Hand-specimen.*—This stuff is yellow-brown, fine-grained, and friable, with a tendency to split off in a platy manner. Small basalt inclusions can be recognised, but the components of the tuff-matrix cannot be distinguished.

*Microstudy.*—The thin section (Pl. I, fig. 4) is composed of sideromelan fragments, chips of dark, nearly opaque hyalo-basalt, and greenish, altered volcanic dust. The average grain-size of the first two materials is 0.5 mm.

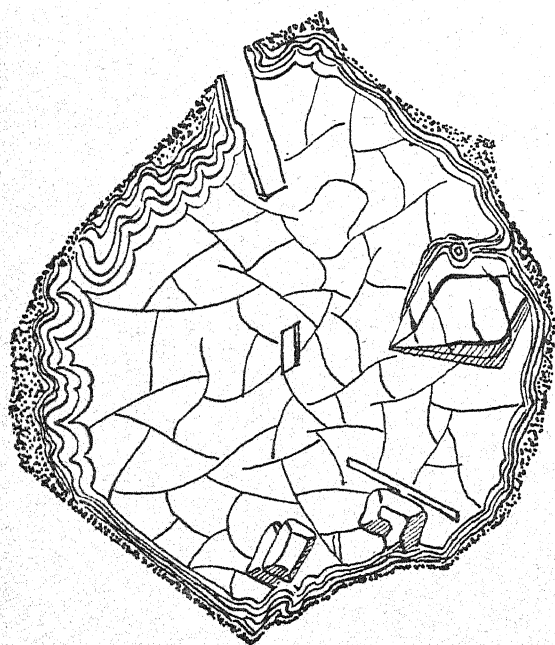


FIG. 3.—A sideromelan grain, about 0.5 mm. in diameter, from the palagonitic tuff (S 115c). The glass contains microlites of bytownite and olivine; marginally it displays incipient palagonitisation.

The sideromelan fragments are for the greater part perfectly fresh, transparent, and pale green-grey in colour; they contain euhedral crystals of bytownite and olivine, and are thus entirely comparable to the typical sideromelan of T 21. Each sideromelan fragment has suffered marginal alteration to a depth of 0.02 mm. to 0.05 mm., fragments less than 0.1 mm. in diameter being usually completely altered. A typical altered sideromelan fragment is delineated in fig. 3. The passage from the fresh vitreous interior to the outer margin of the fragment is marked by a change in colour of the alteration material from pale yellow, through dark yellow, reddish yellow, brown to greenish black. Towards the interior the alteration material frequently displays mammillary structure which passes outwards into obscure banding. The alteration material is essentially isotropic; occasionally, in some of the banded parts, incipient fibrous orientation is revealed by faint double refraction. The alteration which has affected the glass has had absolutely no effect on a marginal microlite of bytownite, and practically none on microlites of olivine. The refractive index of the yellow alteration material is distinctly lower than that of the fresh sideromelan; the minute amount of the former material rendered the isolation of small fragments for exact measurement impracticable. Although it is too early to give the reasons, it may be stated that it is this yellow, essentially isotropic, "colloform"\* material which is regarded as one form of palagonite.

## 3. *Palagonite-Tuff.*

*Occurrence.*—A simple example of palagonite-tuff (R 16) was obtained at about 700 feet from the breccia inlier at Krisuvík, Gullbringu Sýsla. This region is the seat of

\* A term proposed by ROGERS (1917, p. 518) for the spherical, botryoidal, reniform, stalactitic, and mammillary forms assumed by colloidal substances.



vigorous solfataric activity, the aftermath of the Post-glacial volcanic episode which produced the surrounding basaltic lavas.

*Hand-specimen.*—This is a dark-grey, fine-grained, compact tuff in which numerous minute specks of black glass may be discerned.

*Microstudy.*—The thin section (Pl. I, fig. 5) consists of sideromelan fragments which are cemented by their own alteration products. These fragments occupy 25 per cent. of the section by volume, and rarely exceed 0.6 mm. in their greatest dimensions. Their refractive index is 1.606, and in colour, shape, and microlitic content they agree exactly with the typical sideromelan of T 21.

The remainder of the rock is composed of palagonite, which serves both to cement the sideromelan fragments and to line the occasional vesicles, together with a small proportion of calcite. The palagonite presents three facies: surrounding each sideromelan fragment and forming the first lining of each vesicle are found dark bands which are 0.01 to 0.02 mm. wide; as in a previous example (R 21, p. 59) these bands resolve into opaque globulites representing slight ferriferous concentrations. The dark bands pass into palagonitic substance which occupies nearly 75 per cent. of the slide. In colour the palagonite varies from yellow-green to yellow-brown according to the intensity of illumination. For the greater part the palagonite is obscurely fibrous, giving only faint, dull reaction under crossed nicols. To a smaller degree the material is better oriented, giving first-order polarisation colours; this is especially the case in the palagonite which adjoins the dark selvages and the cavity-linings. The average refractive index of both the ill- and the well-oriented types of palagonite is 1.490. In order to distinguish this obscurely fibrous palagonite from the perfectly isotropic, structureless variety which appears in some of the ensuing examples, it is proposed to designate the former as *fibro-palagonite*.

An occasional small patch of calcite is seen occupying a few crevices in the palagonite. It is the latest mineral to form, and its uneven distribution suggests that its formation is unconnected with the palagonitisation process.

Although the passage from sideromelan to palagonite is always sharply defined, it is quite clear that the latter has been formed at the expense of the former. In some of the larger sideromelan fragments microlites may be observed which project from the fresh glass, through the dark bands, into the palagonite; and there are many cases where smaller sideromelans have completely succumbed, leaving their unchanged microlitic contents *in situ*.

*Water Content.*—A sample of this rock yielded the following results:—

H <sub>2</sub> O at 105°	.	.	.	.	.	8.30 per cent.
H <sub>2</sub> O above 105°	.	.	.	.	.	5.60 „
						13.90 „

These figures show for the first time in this paper one of the chief properties of palagonite: namely, its large water content whose greater part is released at moderate temperatures. As 25 per cent. of the rock consists of anhydrous sideromelan and unaltered microlites, the total water content of the rock must be ascribed to the palagonite which, occupying nearly 75 per cent. of the section, thus contains 18.5 per cent. of water. The appearance of the section suggests that the formation of the palagonite has resulted simply from the absorption of water by the sideromelan, and that no further chemical change has taken place beyond a slight segregation and oxidation of iron in the dark bands and an incipient fibrous crystallisation of the gel-material formed by the hydration.

If this be so, the composition of this palagonite differs from that of the sideromelan from which it is derived only in that the former is slightly poorer in iron and notably richer in water than the latter. There are, therefore, grounds for believing that the fall in refractive index from 1.606 in the sideromelan to 1.490 in the palagonite resulted mainly from a gain in water, assisted in a minor degree by a loss in iron.

*Occurrence.*—A specimen (T 83) somewhat similar to the previous example was taken at about 2200 feet from the N. bank of the Markarfljót, where it skirts the northern margin of the Hraftinnuhraun which lies 3 miles W. of the ice on the Torfajökull. The palagonite-tuff occurs as a dyke-like "intrusion-tuff" cutting greatly altered rhyolite or acid breccia. The alteration suffered by the country rock, and also probably by the palagonite-tuff, has resulted from the still active hot-spring and fumarolic action of that locality which followed the effusion of the Post-glacial obsidian of the Hraftinnuhraun.

*Hand-specimen.*—The rock is friable, greenish black, and exceedingly fine-grained; its fracture is hackly and of sub-resinous lustre. Except for a few included fragments of slaggy hyalo-basalt, the specimen is apparently homogeneous.

*Microstudy.*—The section (Pl. II, fig. 1) consists of 35 per cent. of sideromelan and 65 per cent. of alteration material. The sideromelan fragments are pale brown in colour and somewhat vesicular; they display ash-structure, the average size of the fragments being 0.2 mm.; the refractive index of the glass is 1.610.

As in the last case, there is a slight darkening of the margins of the sideromelans due to the separation of opaque globulites and a copious formation of obscurely birefracting palagonite. This material is greenish brown; in small fragments the colour becomes paler with decreasing size. For the most part the highest powers reveal no structure in the palagonite, and therefore the obscure birefringence is referred to incipient, submicroscopic crystallisation. Occasionally when occurring as vesicle-linings or along lines of contact between adjacent sideromelans, well-defined fibrous development is observed; this fibro-palagonite is associated with a minute amount of indeterminable zeolite. The refractive index of the palagonite varies slightly; its mean value is 1.490. Small fragments treated with HCl are immediately bleached with the formation of a solution deeply stained with ferric chloride. On pressing the bleached fragments with a needle they fall into pieces which are bounded by smooth curves similar to the cracks in the fresh sideromelan.

*Water Content.*—This specimen gave the following values:—

H <sub>2</sub> O at 105°	10.40 per cent.
H <sub>2</sub> O above 105°	4.65 "
	15.05 "

As 35 per cent. of the section consists of sideromelan similar to the proved anhydrous sideromelan of T 21, the water content of the remaining 65 per cent., represented by palagonite with accessory zeolite, is 23.5 per cent. Again the estimations show that the major proportion of this water is released at 105°.

*Occurrence.*—A specimen of palagonite-tuff (V 9) was collected a few feet above sea-level from the S. end of Viðey, an island lying 3 miles E.N.E. of Reykjavík. In this locality palagonite-tuffs and -breccias, associated with globular basalts of intrusive aspect, reach an estimated thickness of 700 feet.\*

\* The geology of this island was recently described by the Author, 1926.



*Microstudy.*—The section (Pl. II, fig. 2) consists essentially of sideromelan, palagonite, and zeolites. Sideromelan occupies 8 per cent. of the section; it is deeper brown in colour, and therefore probably richer in ferric oxide than the type sideromelan; its refractive index is 1.605. This brown glass contains an occasional microlite of olivine and plagioclase and is sometimes traversed by dark flow-bands. It is thus similar to the fresh glass of the Viðey palagonite-tuff recently described, and therefore it may also contain up to 4 per cent. of water and thus be eligible for the designation "hydrotachylyte" which was proposed for such a glass.\*

The palagonite which occupies 85 per cent. of this rock is mostly of a clear yellow, perfectly isotropic, gel-like variety; its minimum refractive index is 1.520. It forms uniform margins around the larger sideromelans and completely replaces the smaller ones. The passage from sideromelan to palagonite is again defined by a dark line of opaque iron-bearing globulites. Along lines of junction, and within vesicles in completely palagonitised sideromelans, the yellow gel shows aggregate birefringence accompanied by a change of colour to rich reddish brown or greenish red, and the development of an obscurely fibrous or scaly structure. This alteration material is indeterminable; the reddish brown and greenish colours suggest, however, that the birefracting material may represent an incipient separation of limonite and chlorite. The remaining 7 per cent. of the section is occupied by zeolites which are manifestly the last minerals to form. They are always associated with the birefracting limonitic or chloritic substance; they appear to be the joint alteration products of the isotropic gel. At least three species of zeolites are present. One variety is quite isotropic and has a refractive index of 1.480; it is identified with faujasite. Another is isotropic or faintly birefringent, with a refractive index lying slightly but distinctly above 1.480 and below 1.490; this is analcite. The third variety is isotropic and lies between 1.520 and 1.530; it thus agrees with the mineral recently described from Viðey,† and therefore for the reasons given in that description it may be regarded as an impure potash analogue of analcite.

*Water Content.*—A sample of this rock yielded the following result:—

H <sub>2</sub> O at 105°	.	.	.	.	.	10.10 per cent.
H <sub>2</sub> O above 105°	.	.	.	.	.	8.85    "
						18.95    "

Allowing 4 per cent. of water to the sideromelan, which appeared to be in this case a hydrotachylyte, and 17 per cent. to the zeolites, on the assumption that faujasite and analcite were present in equal amounts, the aggregate water content of the gel-like palagonite and the subordinate birefringent variant works out at 21 per cent. Here again more than the half of this water was released at 105°.

#### 4. Palagonite-Rock.

*Occurrence.*—A specimen of palagonite-rock (T 12), as defined on page 56, was collected at about 320 feet from a bed in the massive series of palagonite-breccias which is exposed in the gully at Austurlið, 4 miles S.W. of Geysir.

*Hand-specimen.*—In this rock large and small chips of dull, microlitic hyalo-basalt and minute specks of black, lustrous sideromelan are seen cemented by a copious reddish matrix which has a resinous appearance when freshly fractured.

\* Author, *op. cit.*, p. 455.

† *Ibid.*, pp. 454-5.

*Microstudy.*—The section (Pl. II, fig. 3) consists of hyalo-basalt, sideromelan, palagonite, and zeolites. Chips of hyalo-basalt, which occupy 12 per cent. of the section, have a tachylytic base charged with plagioclase microlites. This opaque glass has not been in the slightest affected by the palagonitisation process. Sideromelan, whose proportion is 5 per cent., is represented in a few relics completely surrounded by palagonite. The glass is brown and translucent with a refractive index of 1.612. It is netted with the usual curved cracks and it contains microlites of olivine and bytownite. The margins of the sideromelans, where they pass into palagonite, are darkened with the formation of opaque, iron-bearing globulites.

Palagonite occupies 76 per cent. of the section; it is clear and yellow and has a minimum refractive index of 1.500. For the greater part the material has a gel-like appearance and is perfectly isotropic. It is frequently banded in various shades of yellow, the banding running parallel to the outlines of the sideromelan relics. Within the palagonite crystals of olivine and microlitic aggregates of plagioclase may be seen; the sideromelan which originally served as a base for these microlites has been largely or completely palagonitised. It is noteworthy that the microlites have lost none of their freshness in the process.

The isotropic palagonite has been partly altered with the production of a pair of complementary minerals. Firstly, along lines which in many cases appear to represent the original outlines of the sideromelans, strings of a pale-green, fibrous mineral have formed. As these strings are only 0.01 mm. wide, exact identification is not feasible. The colour and structure indicate that the mineral is a chlorite. Secondly, these chloritic vermiculites pass into a colourless zeolite which occupies 7 per cent. of the slide. This mineral has very low birefringence, and its mean refractive index lies midway between 1.490 and 1.503. It is, therefore, identified with stilbite ( $\alpha=1.494$ ,  $\beta=1.498$ ,  $\gamma=1.500$ , LARSEN). In addition to this vermicular form of alteration, the isotropic palagonite has suffered a minor amount of spherulitic crystallisation. Often the spherulites are composed of a chloritic shell with a core of stilbite. Sometimes the spherulites consist of fine radial fibres of palagonite which has crystallised without chemical change.

*Water Content.*—A sample of this rock gave the following values:—

H <sub>2</sub> O at 105°	14.40 per cent.
H <sub>2</sub> O above 105°	5.30 ..
	19.70 ..

Allotting 18 per cent. to the stilbite and the remainder to the palagonite, together with the small amount of chlorite in the proportions given by their respective volume proportions, the water content of the palagonite with the accessory chlorite works out at 24 per cent. Again the major proportion of this water was liberated at 105°.

As the following and final example is the most altered specimen in the collection, and the one in which the palagonitisation process is perhaps the most clearly traceable, it will be rather fully described.

*Occurrence.*—This rock (S 30) was collected near the S. shore of the Hvalfjörður from a massive bed underlying the Glacial lavas of the Múlafjall.\*

*Hand-specimen.*—In this rock vitreous particles can rarely be distinguished from

\* The field relations of this occurrence of palagonite-rock are described and figured in a paper by the Author, 1926, pp. 452-3 and fig. 7.



matrix. The specimen is dark greenish black in colour, and a freshly broken surface has a rather smooth, homogeneous appearance and a resinous lustre. These, it will be remembered (p. 54), are the characters which VON WALTERSHAUSEN ascribed to *Palagonitfels*.

*Microstudy*.—In the section (Pl. II, fig. 4, in ordinary light, Pl. II, fig. 5, under crossed nicols) it is seen that the rock has suffered extensive alteration. The slide consists of sideromelan, palagonite, chlorite, and zeolites. Fresh sideromelan, whose proportion is only 3 per cent., occasionally occupies the central areas of larger vitreous fragments which have been otherwise completely altered. Its colour is chocolate-brown, indicating a notable ferric-oxide content, and its refractive index is 1.615. It is free from opaque patches, but it contains a few microlites of olivine and plagioclase. In observable characters this glass compares more closely with the Viðey sideromelan (p. 63) than with the Gullfoss material (p. 56).

Palagonite occupies 76 per cent. of the section. It has almost completely replaced the original sideromelan. In many cases the networks of curved cracks proper to the sideromelan have been preserved in the palagonite, which in some cases also contains microlites of olivine, which are no less fresh than those in the unaltered sideromelan. Palagonite of an originally more mobile nature—*i.e.* in a more highly hydrated colloidal condition—cements the replaced sideromelans into a coherent whole. This accounts for the almost homogeneous, smooth, resinous appearance of the fracture surface in the hand-specimen. The palagonite is isotropic and its minimum refractive index is close to 1.500. Where it has replaced sideromelan, it is apt to be cloudy and yellow to yellow-brown in colour; where it fuses the replaced sideromelans together it assumes the form of ideal gel-palagonite, which is clear and structureless, and has in this case a pale yellow-green colour.

The palagonite has partly crystallised with the formation of chlorite and zeolites, which minerals occupy respectively 14 and 7 per cent. of the section. This alteration, which has taken place principally within the gel-palagonite, has resulted in vermicular and spherulitic aggregates. The former is displayed in the palagonite films which fuse together adjacent palagonitised sideromelans; the latter is assumed where crystallisation has commenced spontaneously within larger palagonite areas. Chlorites and zeolites are constantly associated; chlorite has clearly formed first, leaving the zeolites to crystallise from the residual constituents of the gel. The chlorite is green and fibrous, the fibres lying radially in the spherulites and normally to the trend of the vermicular areas; it sometimes presents botryoidal surfaces towards the centrally-lying zeolites. The radial fibres are pleochroic, ranging in colour from dark olive-green to pale yellow-green; their mean refractive index is 1.594, their birefringence is about 0.01, and their extinction angle is nearly zero. This association of properties distinguishes the mineral as clinocllore.

The zeolites occupy the circular centres of the chloritic spherulites and the central sinuous areas of the vermicular patches. An isotropic and an anisotropic variety can be distinguished. The refractive index of the isotropic zeolite is slightly above 1.480, and distinctly below 1.490, thus ruling out all species except analcite ( $n=1.487$ ) and faujasite ( $n=1.48$ ). Other optical tests failing, a consideration of the analysis which follows indicates that faujasite, with its lime-content and its low soda and high water, is likelier than analcite. The refractive index of the anisotropic zeolite is faintly below 1.503, and distinctly above 1.490. Comparisons with fragments of known zeolites lying within this range indicated stilbite.

*Chemical Composition.*—A sample of this rock gave the values listed under I. in the following table:—

	I.	II.	III.
SiO <sub>2</sub>	35.34	46.83	46.39
Al <sub>2</sub> O <sub>3</sub>	11.15	14.78	16.27
Fe <sub>2</sub> O <sub>3</sub>	10.28	13.62	1.35
FeO	2.19	2.90	9.96
MgO	6.52	8.64	9.77
CaO	7.01	9.29	13.00
Na <sub>2</sub> O	0.16	0.21	1.40
K <sub>2</sub> O	0.19	0.25	0.15
H <sub>2</sub> O +	8.90	...	0.15
H <sub>2</sub> O -	15.50	...	0.10
TiO <sub>2</sub>	2.10	2.78	1.27
P <sub>2</sub> O <sub>5</sub>	0.24	0.32	0.05
MnO	0.22	0.29	trace
CO <sub>2</sub>	none	none	none
S	0.07	0.09	none
NiO	none	none	none
	99.87	100.00	99.86

I. Palagonite-Rock—Hvalfjörður, Iceland; per cent. soluble in HCl, 62.00. Analyst, W. H. and F. HERDSMAN.

II. Analysis I in which water has been deducted and the remaining constituents have been calculated to 100 per cent.

III. Sideromelan. Gullfoss, Iceland; quoted from page 57.

These analyses will be discussed in later sections.

### III. THE NATURE AND ORIGIN OF SIDEROMELAN.

The tuffs examined all contain that type of basalt glass to which VON WALTERSHAUSEN gave the name *Sideromelan*. Although PENCK identified sideromelan with tachylyte,\* the foregoing descriptions will have shown that the following essential difference exists between the two materials. Sideromelan is characterised by translucency in thin section and freedom from ore-minerals; tachylyte, on the other hand, is characteristically opaque, due to incipient or advanced separation of ores. This difference appears to be unrelated to chemical composition. Both materials are vitreous facies of their respective basalt magmas, and therefore show corresponding variations in composition. The striking agreement between the chemical analysis of the Gullfoss sideromelan and that of the sideromelan from the floor of the South Pacific (Table, p. 57) indicates only the similarity of the two parent magmas. The sideromelan of the tuffs of the Val di Noto contains 9 per cent. of alkalis,† as against 1.5 to 2.3 per cent. in the Icelandic and deep-sea examples, and yet the Sicilian sideromelan shows the characteristic translucency. Nor can the translucency of sideromelan be always related to a high primary water content. Although the sideromelan of Viðey was recently found to contain about 4 per cent. of water, which fact, it was thought, was related to the translucency of the glass,‡ the analysis of the more typical Gullfoss sidero-

\* 1879, p. 522.

† WASHINGTON, 1917, pp. 696-7.

‡ Author, 1926, p. 455.



melan gave only 0.25 per cent. of water. Oxidised magmas would tend to produce darker glasses than unoxidised magmas, but an inspection of a number of analyses of tachylyte makes it clear that the  $\text{Fe}_2\text{O}_3/\text{FeO}$  ratio in these glasses is not systematically higher than in analyses of sideromelan. Again the persistent appearance of olivine and plagioclase in that order of abundance in all the known sideromelans, and the constant refractivity of the Icelandic sideromelan, whose refractive index in eight measured cases varied only between the narrow limits of 1.604 to 1.615, are functions of chemical composition, and not specific properties of sideromelan.

The sideromelan centres of the palagonite cores of some manganese nodules dredged from the bottom of the South Pacific\* agree in every respect with the Icelandic sideromelan. The abyssal sideromelan must have originated from submarine eruptions, which mode of eruption would cause ultra-rapid chilling of the extruded magma and cracking and shattering of the resultant glass into angular, non-vesicular fragments. This chilling was evidently sufficiently drastic to inhibit the facile separation of opaque ores and thus to produce translucent sideromelan. Similarly, the tuffs of the Val di Noto, which contain shelly fragments, also resulted from submarine eruptions. In Iceland sea-water cannot have been the chilling agency, as two of the described examples containing typical sideromelan were found far above the 300-foot line of highest submergence; it is significant that these two specimens (Hungurskarð, 2100 feet, p. 58, and Hraftinnuhraun, 2200 feet, p. 62) were taken in close proximity to the present margins of the ice-fields, Tiudfjallajökull and Torfajökull, which are but small relics of the Pleistocene ice-sheet. For this and other reasons given elsewhere,† it appears in the highest degree probable that the production of sideromelan in Iceland was due to the ultra-rapid chilling effect of the Pleistocene ice-sheet on the products of sub-glacial volcanoes.

Sideromelan does not, of course, conform with the criteria of a mineral species, as VON WALTERSHAUSEN thought; this glass has, however, sufficiently well-defined characters to entitle it to be classed as a *mineraloid*, the apt name proposed by NIEDZWIEDZKI‡ for all naturally occurring homogeneous amorphous substances.

#### IV. THE NATURE OF PALAGONITE.

##### 1. *Nomenclature and Status.*

From the description it appears that the general complete sequence of alteration of sideromelan is the following: sideromelan is more or less completely converted into a yellow material which may be either structureless and perfectly isotropic, or obscurely fibrous and birefracting; this material then breaks down into chlorite and zeolite. The examples which contain the yellow material in greatest amount, i.e. the specimens classified as palagonite-rock are those which display the characters ascribed to *Palagonitfels* by VON WALTERSHAUSEN. The yellow material may therefore appropriately be called palagonite. This use of palagonite is also in complete accord with the usage of MURRAY and RENARD, who used palagonite to denote the yellow and red non-crystalline hydration products of sideromelan. To distinguish the isotropic, gel-like variety of palagonite from the feebly birefringent, obscurely fibrous type, the terms "gel-palagonite" and "fibro-palagonite" were proposed and employed. As the two varieties appear to differ only in structure, the suggested terms seem suitable and useful.

\* MURRAY and RENARD, 1891, pl. xvi, figs. 1-4.

† Author, 1926, pp. 460-1.

‡ 1909, pp. 661-63.

As palagonite is not constant in chemical composition it has no claim to recognition as a mineral species; as a definite petrographic entity, however, palagonite is eminently entitled to be classed with sideromelan among the mineraloids of NIEDZWIEDZKI.

## 2. Microscopical and Chemical Characteristics.

Gel-palagonite appears to be the ideal, although rarer, form of palagonite; when completely structureless its only microscopic characters are its colour and its refractive index. While yellow is the most frequent colour displayed, greenish and brownish varieties were observed. The refractive index of palagonite is somewhat variable; a lower limit of 1.50 was found in a number of cases, and isolated cases of 1.52, 1.49, and 1.48 were observed. In one example (T 12, p. 64) gel-palagonite displayed well-defined periodic banding in various shades of yellow, without showing birefringence. As one would expect the gel-form of palagonite is very unstable and readily passes into fibro-palagonite. This crystallisation may be of a submicroscopic order, when its existence is revealed only by obscure birefringence, or it may result in the formation of minute, definitely arranged fibres which are oriented normal to lines of junction between adjacent replaced sideromelans, or around cavities. The birefringence of fibro-palagonite is low, and its measured refractive index is not appreciably different from the average refractive index of gel-palagonite.

In the sections examined areas of palagonite, uncontaminated by sideromelans or by subsequent decomposition products, never reached 1 mm. sq., and therefore the mechanical separation of a sample for analysis was impracticable. Indirectly, however, the analysis of the palagonite-rock, S 30, together with the knowledge of the approximate proportions and composition of the components other than palagonite, give an indication of the chemical characteristics of palagonite.

The water content of five examples of palagonite-tuff and palagonite-rock ranged from 14.20 to 24.40 per cent. From these values and the micrographic measurements, the water content of palagonite was found to range approximately from 18.5 to 28 per cent. In the two palagonite-tuffs which were characterised by abundant fibro-palagonite (R 16, p. 51, and T 83, p. 62), the calculated water contents were respectively 18.5 and 23.5 per cent.; in the two examples of palagonite-rock (T 12, p. 64, and S 30, p. 65), which consisted mainly of gel-palagonite, the calculated water percentages were respectively 24 and 28. It would thus appear that the conversion of gel-palagonite into fibro-palagonite is accompanied by a slight release of water.

In every case the greater proportion of the total water was released at 105°. Although lightly held, the water released at this temperature is not to be regarded as moisture. An analysis of one of MACKENZIE's specimens, which had lain for over a century presumably in dry storage, shows the same feature.\* SİRÖCZ's analysis of the palagonite coating of a sideromelan fragment from Station 276, *Challenger Voyage*, shows only 9.56 per cent. of water;† but this estimation was made on a sample dried at 105°, the water released at this temperature being naturally regarded as hygroscopic. In a partial analysis of palagonite from the same station, DITTMAR reported 13.5 per cent. of water released at 100°.‡ Much of this water was probably in a lightly-held, non-hygroscopic condition. BARUS has shown that 210 grm. of crushed laboratory glass and 50 grm. of water heated at 210° C. for about 12 hours in a sealed steel tube react to form a rigid, resinous water-glass.§

\* Author, 1924-5 (B), p. 312, anal. H.

† *Ibid.*, pp. 456-7, anal. 83.

‡ MURRAY and RENARD, 1891, p. 463, anal. 94.

§ 1900, pp. 164-5.



This glass disintegrated spontaneously after a few weeks. This and other similar experiments convinced BARUS that the water-glass thus produced was strictly a colloidal solution in water, *i.e.* a hydro-gel. In a series of high-pressure experiments in the hydration of acid volcanic glasses, and of artificial glasses of known composition, SCHOTT and LINCK found that at a pressure of 35 atmospheres and a temperature of 243° C., a glass of the composition of a peridotite absorbed 18 per cent. of water in 10 days, while a glass of granitic composition acquired only 5½ per cent. of water in the same time.\* There are thus good reasons, especially when we consider the conditions under which palagonite was formed, for believing that the water in palagonite is present in the form of a colloidal solvent.

In all the sections lines and zones of opaque globulites were observed along the margins of the relics of fresh sideromelan; these globulites are presumably ferri-ferous in constitution, and therefore the hydration of sideromelan is probably accompanied by a slight separation of iron. It was contended that in sideromelan the facile separation of iron-ores was inhibited by drastic quenching, and it is therefore logical that this same component should be the first to precipitate from the unstable gel. The new analysis of palagonite-rock agrees with all previous ones in showing that palagonitisation is accompanied by an almost complete oxidation of the iron in the original sideromelan. The small proportion of ferrous oxide in the analysis of S 30 must belong largely to the chlorite in that rock. This oxidation of iron is in keeping with the fact that colloidal ferric oxides are of frequent occurrence, while ferrous hydrates are unknown.

Comparing analyses II and III (Table, p. 66) it will be seen that the change from sideromelan to palagonite-rock, the latter being calculated to the anhydrous basis, is marked by the loss of 3.71 per cent. of lime. As the palagonite-rock contained a notable amount of zeolites, the lime content of the gel-palagonite must be even lower than that of the whole rock. Other analyses show the same feature to a more marked extent. The calcite-free version of an analysis of palagonite-rock from Krisuvik gives 3.84 per cent. of lime,† and the lime-value of the deep-sea palagonite from Station 276, *Challenger* Voyage, is only 1.88 per cent.‡ BUNSEN already noticed that the lime in the Icelandic palagonite-tuffs, even when his analyses were calculated to the anhydrous basis, was consistently lower than the lime in the normal Icelandic basalt.§ It may, therefore, be concluded that palagonite, when calculated to the anhydrous condition, is poorer in lime than the parent sideromelan.

Considering the alkalis, the new analysis shows that whereas potash remains practically constant there has been a notable loss of soda in the hydration of sideromelan. Again BUNSEN's analyses show the same feature. In eight analyses by him of Icelandic palagonitic rocks, the average figures for the alkalis are 0.86 per cent. of soda and 0.72 per cent. of potash,|| while the average soda and potash percentages in ten recent analyses of Icelandic basalts, excluding those of alkaline tendencies, are respectively 1.97 and 0.57. The loss of some soda, doubtless bleached out as sodium silicate, is therefore a constant feature in the hydration of the Icelandic sideromelan. The deep-sea palagonite, on the other hand, shows a notable acquisition of alkalis from the sea-water.¶

As there is general agreement between the remaining components of palagonite-rock (reduced to the anhydrous basis), and of the parent sideromelan, we may conclude that palagonite is essentially a hydrogel of sideromelan, the hydration being accompanied by an almost complete oxidation of iron and a partial loss in some soluble form of lime and soda.

\* 1924, p. 114 and fig. 2.  
§ 1851, p. 857.

† Author, 1924-5 (B), p. 312, anal. H'.  
|| *Ibid.*, pp. 852-3.

‡ MURRAY and RENARD, *op. cit.*, p. 463, anal. 94.  
¶ MURRAY and RENARD, *loc. cit.*

### 3. The Relation between Refractive Index and Water Content.

The average refractive index of sideromelan, computed from eight closely agreeing measurements recorded in the descriptive section, is 1.61.\* The minimum refractive indices of gel-palagonite in the three examples which contained that material in notable

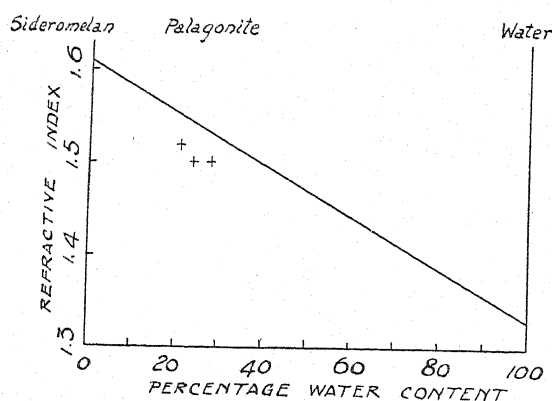


FIG. 4.—Diagram relating the water content and refractive index of palagonite. The three crosses indicate cases of palagonite whose refractive index was measured, and whose water content was indirectly obtained.

amount were 1.52, 1.50, and 1.50, while the calculated approximate water contents of the gel-palagonite in these three cases were 21, 24, and 28 per cent. respectively. The refractive index of water is 1.33. These facts have been plotted on the refractive index: composition diagram, fig. 4. The three points for palagonite fall below the straight line joining the points representing pure sideromelan and pure water, and it is improbable that the relation is strictly rectilinear. As the refractive indices of the three examples of gel-palagonite are minima, *i.e.* values corresponding to the most hydrated portions, the average values will actually lie somewhat higher, therefore nearer to the straight line. For determinative purposes, therefore, the rectilinear relation might be assumed to hold, and thus knowing the refractive index of a palagonite and of the sideromelan from which it was derived, the approximate water content of the palagonite could be readily computed.

### 4. The Conditions which promote Palagonitisation.

There appear to be three possible sources of water in the palagonite; these are meteoric water (including glacial drainage water), hot-spring water, and sea-water. Water acting at atmospheric temperature and pressure must undoubtedly be less potent than water at high temperatures or high pressures. If it can be shown that the palagonite-tuffs were subjected to the action of water under either of the latter conditions, we may discount meteoric water as an unlikely palagonitisation agent.

Of the three examples which were characterised by abundant gel-palagonite, and which compared most closely with the deep-sea palagonite of MURRAY and RENARD, two were collected near sea-level. These rocks were therefore submerged to the extent of about 300 feet during the time of the 100-m. submergence. The third example (T 12, Austurlið, p. 63) was taken too near the 100-m. line to be sure whether it was actually above or below at the time of that submergence. Cold sea-water at high pressure was undoubtedly the palagonitisation agent in the *Challenger* specimens, and it seems certain that this same agency effected the palagonitisation of those Icelandic tuffs which lie below the line of highest submergence. The action of sea-water, it will be remembered, figured prominently in VON WALTERSHAUSEN'S hypothesis (p. 54). The remaining examples of palagonite-tuff and palagonite-rock, including the above-mentioned specimen whose submergence was doubtful, were all found in active hot-spring areas; thus the conclusion which BUNSEN already indicated (p. 55), that hot volcanic waters were the palagonitisation agents in those cases, cannot be resisted. In some cases other combinations of conditions may have obtained. The Hvalfjörður rock (S 30, p. 64), for instance, may have

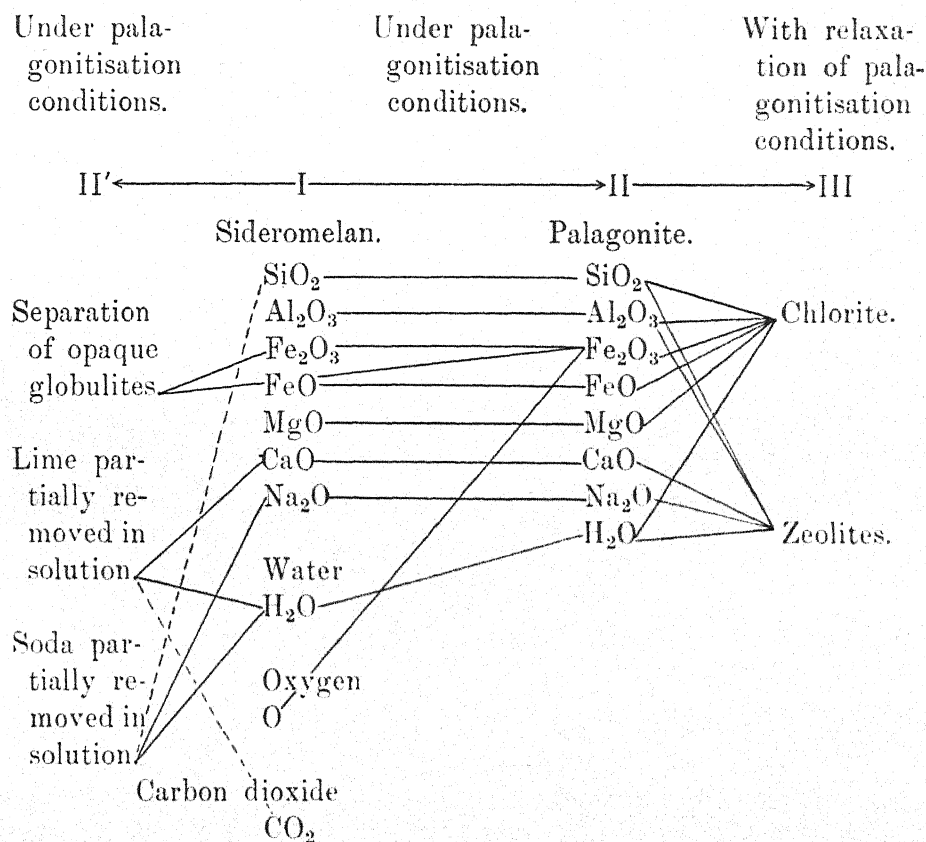
\* Neglecting as insignificant the digit in the third decimal place.



been just submerged when the massive series of overlying basalts were poured out; in that case sea-water may have acted at elevated temperature. Again, the many basaltic intrusions which have entered the Breccia Formation must frequently have caused local heating promoting palagonitisation in sideromelan-tuffs saturated with glacial waters. SCHOTT and LINCK have remarked that the amount of hydration of glasses is increased by pressure, while elevated temperature reduces the amount of hydration but accelerates the reaction.\* It was previously indicated that gel-palagonite appeared to have a somewhat higher water content than fibro-palagonite, and on considering the notes on the occurrence of the various specimens, we find that the tuffs which are characterised by gel-palagonite are those which have been submerged and have therefore been acted on at raised pressure and low temperature, while those which contained dominant fibro-palagonite were always associated with hot springs.

#### 5. The Final Breakdown of Palagonite.

In the two examples of palagonite-rock and in the palagonite-tuff from Viðey p. 63), the development of a pair of final alteration minerals was observed within the palagonite. This alteration sometimes took a composite vermicular form along the junctions between palagonitised sideromelans; sometimes it displayed a spherulitic habit, the



spherulites either growing spontaneously within the palagonite, or commencing as cavity-linings. In each case the vermiculites and spherulites consisted of chloritic materials and zeolites which had formed in that order. In one case clinocllore was identified; in the other cases the exact nature of the chloritic material was indeterminate. Among the zeolites faujasite, analcite, ptilolite, and stilbite were recorded. A consideration of the

\* *Op. cit.*, p. 113.

chemical composition of these two alteration products shows that they contain together all the components of palagonite except ferric oxide. In one case (V 9, p. 63) limonite was indicated among the final products, thus accounting for the ferric oxide in that palagonite. In other cases, where palagonite passed into chlorite and zeolites without the formation of opaque or brown material, we must conclude that the ferric oxide in the palagonite was largely reduced to the ferrous condition before entering into combination as chlorite.

The average water contents of the above chlorites and zeolites is distinctly lower than that of palagonite, and therefore the formation of these minerals will have followed upon a relaxation of the conditions which promoted palagonitisation. Pressure, it was seen, promotes hydration, and therefore relief of pressure will encourage crystallisation to the less hydrous condition. Such a relief of pressure has occurred in the cases of palagonite-rocks which were once submerged and are now above sea-level.

We may now represent graphically the chemical changes which take place in the hydration of sideromelan and in the subsequent breakdown of the resultant palagonite.

The diagram (p. 71) represents the three essential phases in the formation and subsequent breakdown of palagonite. I passes to II and II' under conditions which promote palagonitisation, while II passes to III with relaxation of these conditions. The full lines indicate transferences for which there is good evidence; the broken lines represent transferences for which there is no direct proof. Thus the soda which is partially removed in the passage from I to II' probably went in the form of a soluble sodium silicate, although this could not be definitely established; and the lime which is partially lost at the same time was very probably, but not certainly, in the form of carbonate of lime in solution. This conjecture is made almost a certainty by the fact that several sections of palagonite-tuff, not mentioned in this paper, contained calcite.

#### 6. *Palagonite in Basalts and Dolerites.*

It will have been appreciated that a definite attempt has been made to restrict the definition of the term palagonite and to reinstate it in a creditable position in the nomenclature of petrology. This endeavour would be incomplete without at least a brief notice of a current use of palagonite to denote certain late-magmatic, hydrous, residual materials in some basaltic and doleritic rocks. Palagonite has been used in this sense by TEALL,\* EMERSON,† FERMOR,‡ WADIA,§ and the Author,|| while CAMPBELL and LUNN¶ have recently described as chlorophæite a material which appears to resemble these basaltic and doleritic palagonites.

These materials appear to have many characters in common with the palagonite in the Icelandic tuffs. They have an inconstant basic composition; the iron which they contain is largely in the ferric condition; they are soft and soluble in HCl, and they have a vitreous or colloidal character. In four of the descriptions referred to above, the data are sufficiently complete to permit of a close comparison of these late-magmatic palagonites with chlorophæite, and to determine whether the former are not more closely related to the latter than they are to the Icelandic tuff-palagonite.

A consideration of the tabulated data indicates that what has been named palagonite in basalts and dolerites is really closely related to chlorophæite; and those properties which seem to distinguish basaltic and doleritic palagonite from chlorophæite do not bring the former any nearer to the Icelandic palagonite. Thus TEALL's low  $\text{Fe}_2\text{O}_3/\text{FeO}$  ratio,

\* 1897, pp. 485-88.

§ 1925, pp. 333-1.

† 1905, pp. 103, 104, and 112.

|| 1924-5 (B), pp. 235-6; 1926, pp. 457-8.

‡ 1925, pp. 125-35.

¶ 1925, pp. 435-40.



while tending to estrange the Cape Flora material from chlorophæite, does not the better entitle it to the name palagonite, in which material this ratio is characteristically high. Again, the water contents of I and II, although apparently systematically lower than those of III and IV, are also lower than the average water content of palagonite. But there are more serious objections to this use of palagonite. If the data and arguments of the foregoing pages are considered trustworthy and valid, then palagonite must be re-

	I. Palagonite, Cape Flora, Franz Josef Land;  TEALL.	II. Palagonite, New Reservoir, Holyoke, Mass.;  EMERSON.	III. Chlorophæite (Palagonite), Nagpur, India;  FERMOR,* WADIA.*	IV. Chlorophæite, Dalmahey, Edinburgh;  CAMPBELL.
SiO <sub>2</sub> . . .	35 †	40	35	35
Al <sub>2</sub> O <sub>3</sub> . . .	8	5	1	5
Fe <sub>2</sub> O <sub>3</sub> . . .	12	25	22	12
FeO . . .	15	4	2	9
MgO . . .	7	5	5	5
CaO . . .	1	1	3	3
Na <sub>2</sub> O . . .	4	0	0	2
K <sub>2</sub> O . . .	0	1	0	0
H <sub>2</sub> O . . .	17	17	32	29
Sp. gr. . .	2.4	1.91	1.83-1.84	1.81 ±
Sol. in HCl .	Yes.	Yes.	...	Yes.
Hardness .	1	3	2-2½	1½
Colour in thin section.	Deep brown with green zones.	Deep red-brown.	Dark orange.	Pale green, dark green, brown- green, red.
Reaction under crossed nicols	Minute birefrin- gent fibres and scales.	Isotropic or dim polarisation in broad bands.	Mainly isotropic; feeble anomalous double refraction.	Mainly isotropic; partly in polarising fibres.
Occurrence .	In amygdules, and replacing paler brown glass in basalt.	In lobate patches in gabbroid quartz diabase.	In cavity-linings and amebiform patches in dolerite; re- placing augite.	Replacing olivine in dolerite (tholeiite); in apparently ves- icular patches; in veins.

served for the hydrogel of sideromelan which occurs only in fragmental basaltic ejecta; and palagonitisation must be regarded as a mild hydration process (accompanied by certain minor chemical changes) which takes place at low or moderate temperatures and has no effect on opaque glass or on feldspars or ferromagnesian minerals. The so-called palagonite in basalts and dolerites has arrived at a somewhat similar composition to the Icelandic tuff-palagonite by an entirely different process. In every case these so-called palagonites are either the solidification products of the last, therefore highly differentiated, aqueous liquor of a basalt or a dolerite, or the products resulting from the reaction of this liquor with vitreous or cryptocrystalline mesostasis, or with crystals of ferromagnesian

\* Data collected from both papers. † Chemical constituents to the nearest whole number.

minerals, feldspars, and ores. Thus, instead of using palagonite to embrace chlorophæite and kindred materials formed under the above conditions, as FERMOR\* suggests, the author would recommend, in the light of the new data, that palagonite be reserved for the hydrogel of sideromelan, and that another term be devised for late-magmatic, residual materials in basalts and dolerites.

#### V. SUMMARY OF CONCLUSIONS.

1. The finer-grained beds of the Icelandic tuffs of Early-glacial and later age are either sideromelan-tuffs or palagonite-tuffs.
2. Sideromelan is a black, lustrous, mostly anhydrous basalt glass which is pale coloured and translucent in thin section; it is known only in fragmental volcanic ejecta. In Iceland, sideromelan is a product of drastically chilled, sub-glacially extruded basalt magma. This mode of formation results in the invariable fragmentation of the material and the inhibition of ore-separation producing the characteristic translucency. Sideromelan-tuffs are found near the margins of the present ice-sheets at heights up to and exceeding 2000 feet. Sideromelan may be classed as a mineraloid.
3. The palagonite-tuffs are the older sideromelan-tuffs which have suffered hydration, usually by submersion or by hot-spring action.
4. Palagonite is the hydrogel of sideromelan. It is a yellow, colloidal material containing up to 28 per cent. of water, the greater part of which is liberated at 105° C. When hydration has taken place at low temperatures by submersion, isotropic gel-palagonite tends to form; when hydration results from hot-spring action, obscurely birefracting fibro-palagonite is the main product. The change from sideromelan to palagonite is further accompanied by a partial loss of lime and soda, an almost complete oxidation of iron, and a progressive lowering of refractive index.
5. Palagonite is unstable; it tends to crystallise with a partial loss of water into chlorites and zeolites.
6. It is recommended that the use of palagonite to denote certain late-magmatic, hydrous materials in basalts and dolerites be discontinued.

#### VI. ACKNOWLEDGMENTS.

In conclusion, the writer desires to record his thanks to the Carnegie Trust, whose financial assistance permitted both the joint visit to Iceland and the study of the material treated in this paper; and defrayed a large part of the cost of the illustrations.

The cost of the partial and complete analyses was defrayed by a grant from the Government Grant Committee, to whom the writer would express his indebtedness.

Finally, the author would acknowledge the general assistance and encouragement he has received from his collaborator, Dr G. W. TYRRELL.

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\* *Op. cit.*, pp. 130-1.



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## EXPLANATION OF PLATES.

## PLATE I.

Fig. 1. Sideromelan from the sideromelan-tuff (T 21) which is associated with glacial sediments in the W. wall of the gorge of the Hvítá, at Gullfoss, Iceland. The sideromelan is a very pale apple-green, basaltic glass containing microlites of olivine and anorthite. The absence of opacity in this glass, the feature which distinguishes sideromelan from tachylyte, is due to ultra-rapid chilling ensuring the inhibition of ore-separation. In Iceland this chilling was a result of the magma being extruded sub-glacially. Described on pp. 56-7; analysis on p. 57 (50 diameters).

Fig. 2. Sideromelan-tuff (T 106) from the Hungurskarð, 1 mile N. of the present northern limit of the ice on the Tindfjallajökull, Iceland. Described on pp. 58-9 (55 diameters).

Fig. 3. Sideromelan-tuff (R 21) with zeolitic cement (faujasite and ptilolite), from the agglomerate on the S. side of the Béjarfell, Reykjanes, Iceland. Described on pp. 59-60 (50 diameters).

Fig. 4. Palagonitic tuff (S 115 c), from the Búrfell, 3½ miles S.S.E. of Sandur, Snæfells Peninsula, Iceland. The pale sideromelans show incipient marginal conversion into yellow, mammillary or obscurely banded palagonite. Described on p. 60 (120 diameters).

Fig. 5. Palagonite-tuff (R 16) from the active solfataric region at Krisuvík, Gullbringu Sýsla, Iceland. The pale sideromelan fragments are cemented by copious yellow-green to yellow-brown fibro-palagonite which has formed at the expense of the sideromelan. Described on pp. 60-61 (120 diameters).

PLATE II.

Fig. 1. Palagonite tuff (T 83) from the fumarolic region on the N. bank of the Markarfljót, where it skirts the northern margin of the Hraftinnuhraun, 3 miles W. of the edge of the ice on the Torfajökull, Iceland. The pale sideromelans have been largely converted into greenish-brown fibro-palagonite. Described on p. 62 (80 diameters).

Fig. 2. Palagonite-tuff (V 9) from near sea-level at the S. end of Viðey, 3 miles E.N.E. of Reykjavík, Iceland. The larger sideromelans have been converted largely, and the smaller ones totally into clear yellow, isotropic gel-palagonite, which in turn has partly broken down into a chloritic material and zeolites (faujasite, analcite, etc.). Described on pp. 62-3 (80 diameters).

Fig. 3. Palagonite-rock (T 12) from the gully at Austurlið, 4 miles S.W. of Geysir, Iceland. The section consists mainly of gel-palagonite which has almost completely replaced sideromelan. The palagonite, which displays well-defined periodic banding, has broken down to some extent to form chlorite and analcite. Described on pp. 63-4 (80 diameters).

Fig. 4. Palagonite-rock (S 30) from below the glacial lavas of the Múlafjall, near the S. shore of the Hvalfjörður, Iceland. The rock consists almost entirely of gel-palagonite which has suffered extensive spherulitic conversion into clinocllore, fauvasite, and ? stilbite. Described on pp. 64-5; analysis on p. 66 (120 diameters).

Fig. 5. The same area as Pl. II, fig. 4, photographed under crossed nicols. This figure shows the isotropic character of gel-palagonite and fauvasite and the slightly inclined extinction-cross of clinocllore in spherulites (120 diameters).



Dr G. W. TYRRELL and Dr MARTIN A. PEACOCK: "The Petrology of Iceland."—PLATE I.

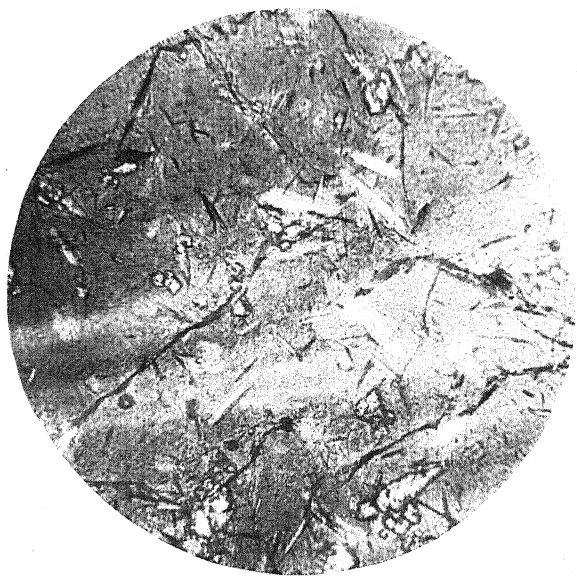


FIG. 1.



FIG. 2.

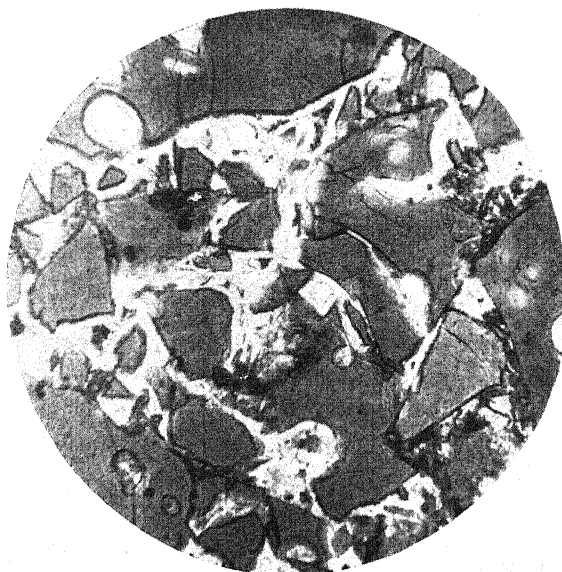


FIG. 3.

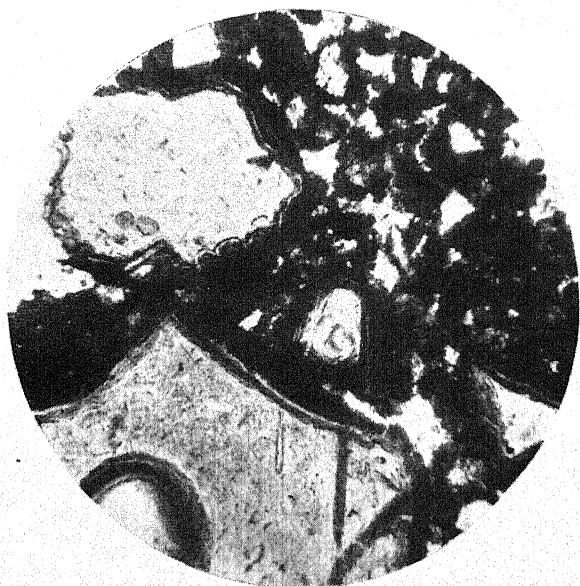


FIG. 4.



FIG. 5.





Dr G. W. TYRRELL and Dr MARTIN A. PEACOCK: "The Petrology of Iceland."—PLATE II.



FIG. 1.

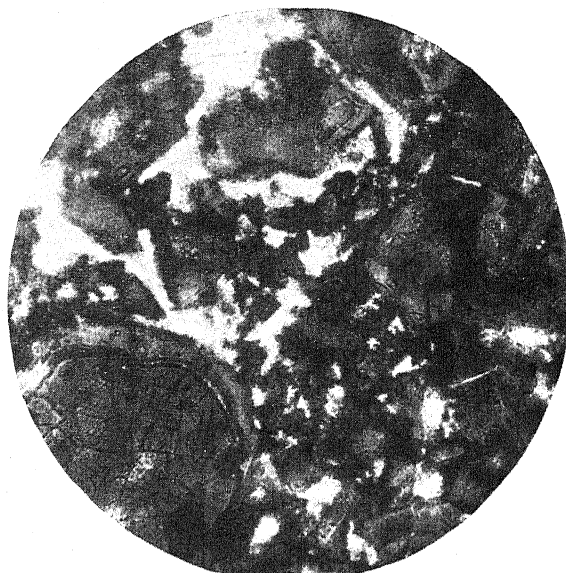


FIG. 2.

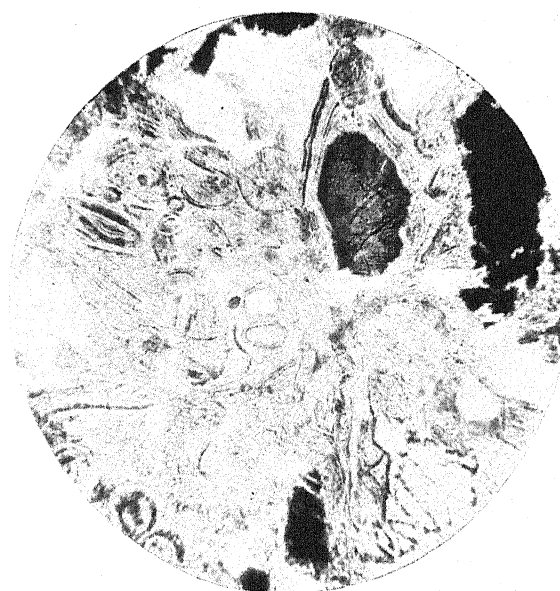


FIG. 3.



FIG. 4.

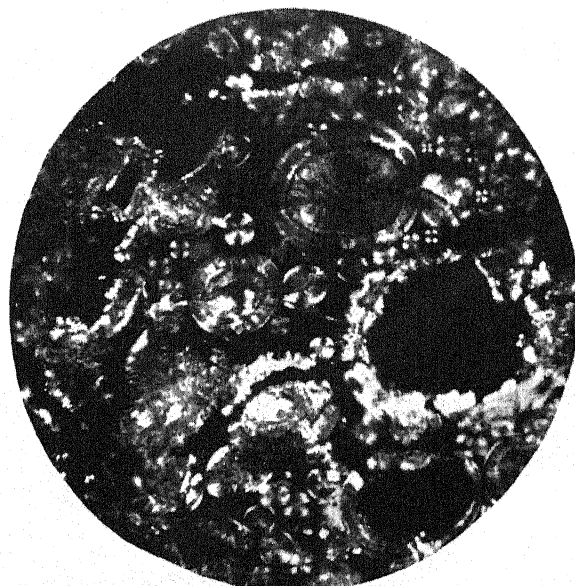


FIG. 5.





IV.—The Development of the Vascular System in the Human Embryo prior to the Establishment of the Heart. By Donald M'Intyre, M.B.E., M.D., F.R.C.S.(Ed.) F.R.F.P. & S.(Glas.), Assistant to the Muirhead Professor of Obstetrics and Gynaecology, University of Glasgow; Assistant Surgeon and Pathologist, Royal Samaritan Hospital for Women, Glasgow; Assistant Physician, Royal Maternity and Women's Hospital, Glasgow. *Communicated by Professor T. H. BRYCE, F.R.S.* (With Three Plates and Eight Text-figures.)

(MS. received May 24, 1926. Read June 21, 1926. Issued separately November 11, 1926.)

Our knowledge of the earliest stages of blood-vascular development in the human embryo suffers from a dearth of suitable material. Early human specimens are not frequently available for examination; many are pathological; some, although of value for other purposes, are not sufficiently well preserved to furnish observations on angiogenesis; direct microscopic observation of the tissues while undergoing development cannot be carried out as is possible, say, in the chick embryo. Our knowledge of the process must be based on descriptions of separate specimens representing different stages. Individual specimens, therefore, are worthy of careful record.

I have the opportunity of recording the blood-vascular development in two specimens of the presomite stage, viz. the TEACHER-BRYCE No. 2 and the M'INTYRE. These two specimens have recently been described by Professors BRYCE and TEACHER, and the reader is referred to their papers for the anatomical detail. The development of the system of which this paper treats has been considered in broad principle by BRYCE, but only in so far as it completes the anatomical description. Herein it is proposed to set down in some detail the vascular picture as it appears in these specimens.

The data accumulated will then be considered alongside that supplied in descriptions of other early embryos. Many controversial points are encountered in the literature. Take, as an example, the origin of the earliest angioblastic tissue. Does it arise from mesoderm or from endoderm? Isolated fixed specimens do not lend themselves readily to a solution of this problem, and recourse has been had to experimental work on living material. Needless to say, no human material is available. Of this type of work the most recent and most important is that of Professor SABIN, who finds by direct observation of the blastoderm of the chick that the angioblast is developed from mesoderm. WANG's work on ferret embryos, wherein specimens of different ages are followed through successive stages, is another recent addition to our knowledge of vascular development.

While material, other than human material, may be employed to settle general questions, the detail of early vascular development must come from human specimens. STREETER, in describing his specimen (Mateer), pays particular attention to the vascular system. INGALLS (1920) describes, with special reference to the vascular system, an embryo representing a very important stage in the development of this system, viz. the stage at which the vascular elements in the different regions (chorion, yolk-sac, blastoderm) have commenced to establish connection with one another, although the process is not yet completed. His description is most beautifully and clearly illustrated. This specimen is of special value when considered alongside the older of the two specimens to be dealt with in this paper.

Only one paper embodies the views of an observer after personal examination of a series of early human ova. I refer to BREMER's article of 1914. His views must be regarded as holding a most important place in the literature. While reference in detail will be made later in this paper to the work of SABIN, WANG, STREETER, and others, to appreciate properly the bearing of this new material on BREMER's work it will be necessary at once to state some of the conclusions at which he arrives.

After examining many of the known specimens, BREMER concludes that "the earliest blood-vessels arise separately in the yolk-sac and in the body-stalk, by multiple anlagen. The anlagen in the body-stalk (and perhaps also in the yolk-sac, *cf.* JUNG's fig. 17) are funnel-shaped ingrowths of the surface mesothelium. . . . By partial fusion of the walls of an ingrowth a portion of the coelom, still bordered by mesothelium, may be cut off as a separate cavity, lying deep within the substance of the body-stalk. The endothelium seems to arise either (a) by delamination from the walls of such a detached portion of the coelom, or (b) by direct extension, in the form of an angioblast cord, from the mesothelial ingrowth. . . . Extension within the limit of the areas covered by the mesothelium is achieved by confluence of the detached portions of the coelom, or union of the cords; the result is a net comprising the various vascular units. Extension into the chorion, where the mesothelial layer is absent in the early stages, appears to be by direct centrifugal growth of the angioblast cords, without the addition of new elements from the surrounding mesenchyma. . . ."

After delamination of the endothelium we have, therefore, spaces regarded as isolated portions of the coelom, referred to by BREMER as "unlined spaces," containing strands which will go to form endothelium.

#### TEACHER-BRYCE OVUM NO. 2.

The ovum was found by Professor TEACHER at autopsy. The fixation and histological detail are excellent. This is worthy of emphasis, as it renders the specimen particularly valuable in supplying data regarding the many unsettled questions which arise in connection with vascular development. The following summary of measurements and anatomical notes indicate the stage of development reached:—

External dimensions of chorionic vesicle (roughly)	. 4 × 4.5 × 3.5 mm.
Cavity of chorion	. 2.8 × 2.6 × 2.25 mm.
Blastoderm	. 0.2 × 0.1 to 0.15 mm.
Yolk-sac	. 0.05 to 0.2 × 0.396 mm.
Amniotic cavity	. 0.09 to 0.1 × 0.16 mm.

The yolk-sac, greater in size than the amnion, is conical in shape and is prolonged in a tapering process to form a second attachment to the chorion.\* An allantoic diverticulum is not recognised. The villi are well developed and show simple but not extensive branching. The sections are 6.25 microns thick.

BRYCE in his memoir refers to the part of the chorionic vesicle at the point of entrance as the "vegetative pole," and the area opposite on the decidua basalis and in the vicinity of the body-stalk as the "embryonic pole." These terms will be employed similarly here.†

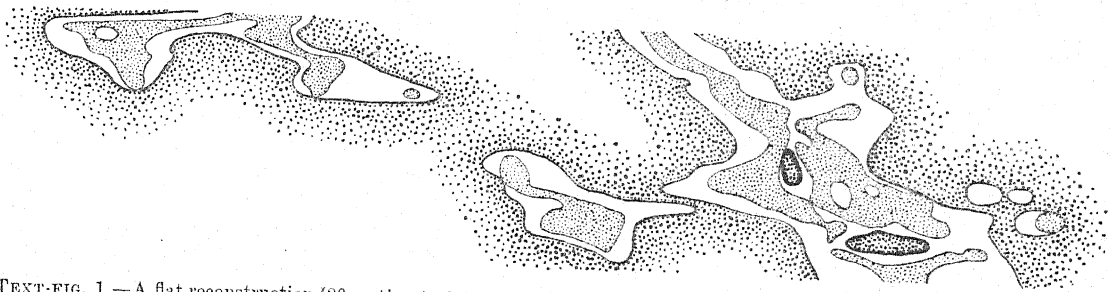
\* An excellent idea of the general anatomy of this ovum may be obtained by reference to BRYCE's memoir, pl. i, fig. 4.  
 † TEACHER uses "Closing Pole" and, following GRAF SPEE, "Implantation Pole."



*Chorion.*

Before considering the question of vascular development, reference to the general arrangement and structure of the chorionic mesoderm is necessary. This layer has on its inner surface, and in direct contact with it, the granular reticular coagulated contents of the blastocyst which have been described by BRYCE. This material which had settled towards the embryonic pole lies on the inner surface of a very loosely arranged tissue, and makes it difficult to define the inner limit of the mesoderm. The nuclei of the chorionic mesoderm are of varied form, spherical, ovoid, or rod-shaped, and the size varies within limited range. This tissue cannot be resolved into individual cells, although usually there is a condensation of protoplasm around the nuclei. Most often this takes an elongated form with tapering extremities and with the long axis corresponding to that of the contained nucleus. A distinct cell-envelope is absent. The rod-shaped nuclei are most numerous at the inner aspect of the chorionic mesoderm, the rounded variety at the outer margin.

While the connecting stalk has a practically complete layer of mesothelium, the mesoderm at the embryonic pole and frequently at some little distance from the stalk



TEXT-FIG. 1.—A flat reconstruction (20 sections) of the angioblastic strands and spaces in an area of the chorionic mesoderm at the embryonic pole directly opposite the operculum of the Teacher-Bryce ovum No. 2. The reconstruction is equivalent to a view at right angles to the microscopic sections, or to a silhouette view through the chorionic membrane.

shows small patches of what resembles a mesothelial covering (Pl. I, fig. 1). These small patches are not continuous with the mesothelium of the connecting stalk. Where they exist there is a zone of fine reticulated structure devoid of nuclei separating them from the underlying mesoderm.

Round the wall of the chorionic vesicle spaces occur in the mesoderm. In many of these there are present strands of nucleated protoplasm staining deeply with eosin. The significance of these strands and their relationship to the spaces in which they lie requires consideration.

The spaces form a complicated branching network disposed parallel to the trophoblast layer (text-fig. 1). The system is not continuous throughout. Some channels disappear when traced through several sections, while a few appear to open into the lumen of the chorionic vesicle. The walls of the spaces cannot be said to have an endothelial lining. Now and then a rod-shaped nucleus is seen in the wall, but this is no more frequent than in the mesoderm elsewhere. More often the nuclei in the wall of a channel are ovoid and without any more definite condensation of protoplasm around them than exists in relation to the mesoderm nuclei in general. Often no nuclei are seen in one wall of the space for a considerable distance, and this occurs mostly on the side towards the lumen of the vesicle. Again, at times a space appears in part of its course without any nuclei in the immediate vicinity of its walls, and the walls themselves are ragged and irregular. One is left with the definite impression that these are spaces which have opened up in the mesoderm and that there is very little, if any, special

condensation of the mesoderm cells around them. The spaces are present principally in the inner region of the mesoderm, although occasionally they are seen near the trophoblastic covering but are never in direct relationship to it. They are not continued into the mesoderm of the villi. They form a striking feature at the embryonic pole, where they are of greatest calibre. Passing round the blastocyst towards the vegetative pole they are seen to diminish in size, until near the operculum where the mesoderm layer is thin they are infrequent and inconspicuous. At the area on the equator of the blastocyst, where the prolongation of the yolk-sac is attached, they are specially large, interrupting the gradual transition from pole to pole. Where patches of mesothelium-like cells exist, no connection of these with the spaces could be made out.

The nucleated strands in the chorion can be recognised only in relation to the spaces or channels described above (Pl. I, fig. 2). In its typical form a strand consists of an elongated syncytial mass running in the lumen of a space. The protoplasm is small in amount and drawn out into a thin thread between nuclei where these are far apart. The protoplasm stains more deeply with eosin than that around the ordinary mesoderm nucleus. In the neighbourhood of the base of the stalk the protoplasm in places may swell out to contain several nuclei which are oval, rounded, or kidney-shaped, and are a little more regular in size than those of the mesoderm. The protoplasm has usually a clean-cut edge, but now and then the surface appears to have very minute thread-like processes passing from it. The nuclei where the strand is a more slender one are elongated and sometimes show a curved axis. In individual sections a strand may appear to be entirely free in the lumen, but often a narrow attachment to the wall is present (Pl. I, fig. 2). This attachment may be broader, and at times the strand forms one side of the wall of the space. Where a strand of some length appears, it may run obliquely from one side of the space to the other with attachment at either end.

Now and then a strand is seen to terminate free in a space, and this takes the form of a tapering, sometimes curved, tail-like ending. Plate I, fig. 3 represents a high-power drawing with the aid of the stereoscopic eyepiece, by Mr A. K. MAXWELL, of a medium-sized strand. Like the spaces in which they lie, these syncytial strands do not form a continuous network. The larger ones branch and form isolated network systems throughout the mesoderm. No continuity of these structures with the mesothelium-like patches on the inner surface of the mesoderm could be established. Excepting one strand described and figured by BRYCE in his memoir (Pl. iv, fig. 18), to which reference will be made later in this paper, these structures do not show the presence of a lumen. The arrangement of the nuclei and the general contour of many of the strands strongly suggest the possible, early appearance of a lumen. SABIN has observed the actual differentiation of mesoderm to angioblast in the blastoderm of the chick, and the angioblastic tissue unites to form cords of cells. STREETER describes, in the chorion of a human embryo, multinucleated, protoplasmic strands and intervening stages up to complete endothelial tubes.

In the next specimen to be described the earliest representation of vessel-forming tissue is found in solid, deeply-staining, nucleated strands, and the intervening stages up to corpuscle-containing channels are present. One has little hesitation, therefore, in concluding that these nucleated protoplasmic strands described are angioblastic strands.

The spaces or channels in the chorionic mesoderm possess no lining which might suggest that they are, or, in themselves are likely to form, vessels. Although it cannot be denied that some of these spaces communicate with the extra-embryonic coelom, such communications are not numerous in comparison with the many spaces present. The chorionic mesoderm has a loose open arrangement of its tissues, and its inner limit is indistinct. No matter what type



of spaces or cavities were distributed generally throughout this zone, it would be surprising if a few of these did not communicate, as mere accidental occurrences, with the extra-embryonic coelom. On the other hand, the spaces, whether they communicate with the coelom or not, may have been produced by the identical process which brought about the formation of the coelom. The extra-embryonic coelom in this ovum is established, and the arrangement of the spaces makes it unlikely that they will go to produce its further development, so that they are not a part of the process of coelom formation. The fact that most of the spaces do not communicate with it merely indicates that they are not formed by tubular extensions of the coelomic cavity into the chorionic mesoderm. It should be noted also that they never contain any of the granular coagulum present in the coelomic cavity.

A point which is worthy of consideration is the possibility that these spaces have been merely potential during life, and that they have become actual only in the course of preparation of the specimen. Against this we have the absence of distortion of the tissues in their vicinity and the presence of many with a wide and sharply defined lumen. In the preparation of the specimen slight exaggeration of the spaces, present as actual channels in the living state, may have occurred.

The solid protoplasmic strands in these channels are regarded as angioblastic tissue, they are destined to form endothelium and blood corpuscles, as will be seen in the earlier forms in the chorion of the M'Intyre ovum. There is no evidence to support the possible view that the spaces represent vascular channels and that the strands will go to form blood-cells only.

I venture to suggest in explanation of these channels that they are present to facilitate the rapid diffusion of material for the nutrition of the tissues of the ovum. As might be expected, they are found in direct relation to the angioblastic tissue which at this stage requires special provision for its rapid, even precocious, development. They persist only for a very short period because when the extra-embryonic coelom is fully formed, and the vesicle has become larger, the chorionic mesoderm is relatively a much thinner layer and has a greatly increased area. This improvement in facilities for diffusion having been established, the spaces disappear, the vascular elements lie in direct contact with their surroundings, and the chorionic mesoderm as a whole becomes a more condensed layer. The M'Intyre ovum will show this stage completed.

#### *Body-stalk.*

Angiogenesis in the base of the stalk takes the same form as in the chorion. Here the mesoderm forms a considerable mass, but is broken up by the spaces which contain the angioblastic strands. The spaces are irregular in shape and taper off in several directions in the plane of the chorion into the more regular channels seen in that membrane. The contained strands are here less slender. Sometimes quite a mass of protoplasm with numerous nuclei is present, and this, at intervals, shows a broad attachment to the wall of the space. Again, the mass may appear broken up into small portions containing one, two, or three nuclei only. The spaces in the stalk come into close relationship with the amnion duct, but, close to the amnion itself—that is nearer the embryonic end of the stalk—another mode, or perhaps phase, of blood-vascular development is found. Collections of cells situated in the mesoderm of the stalk have all the appearances of early blood-cells. The two largest of these can be traced through four and five sections respectively. The remainder are smaller and consist of four to six cells. The cells stand out from the surrounding mesoderm by virtue of their nuclei being more rounded and more regular in size than those of the mesoderm in general, also, each nucleus has a narrow rim of deeply-stained protoplasm making the individual

cells spherical. Although the protoplasm is not frankly hæmoglobin-coloured, the deep staining is highly suggestive. The spaces in which these cell masses lie differ from those already described in that they have the lumen almost completely filled by the contained cells. Further, there are cells arranged around the wall, in appearance similar to those in the lumen of the space except that here and there the nucleus is elongated and is disposed along the wall. In one section (Pl. I, fig. 4) the collection of cells appears as if it had been formed by a sinking in from the surface in the direction indicated by the arrow. The space in which the cells lie would thus be regarded as continuous with the coelom. Traced from this section, the space with its contained cells is found to run obliquely to the middle of the stalk in a direction away from the chorion. This arrangement and the appearance of the cells gives quite a different picture to that of the spaces at the base of the stalk and in the chorion.

If the interpretation that the space mentioned above communicates with the coelom is correct, it lends support to BREMER's view that funnel-shaped ingrowths of the mesothelium of the body-stalk occur in association with the earliest stages of vessel-formation.

#### *Yolk-sac.*

The yolk-sac is cut very obliquely to its long axis. For the most part both endoderm and mesoderm are composed of a single layer, and in both of them localised thickenings are seen sparsely scattered throughout. In the mesoderm this takes the form of a duplication of the single layer with a suspicion of radial arrangement of nuclei. Otherwise they differ no way in appearance from the rest of the layer in which they lie. There is nothing which enables one to label these collections "angioblastic."

In one instance situated in the mid-lateral wall a small mass lies between the mesoderm and endoderm (Pl. II, fig. 5). This mass, which is present through seven sections, at one end in two sections shows quite definite continuity with mesoderm (Pl. II, fig. 6). Elsewhere it lies free between the two layers. It is clearly a mass of mesoderm which has projected in towards the endoderm, and has then made its way along between the two layers. There is no hæmoglobin coloration, but the protoplasm stains fairly deeply, and the nuclei are more spherical than the adjacent nuclei of the mesoderm and endoderm. The nuclei are not arranged in any definite manner, and the mass cannot be resolved into individual cells. There is no actual proof that this is the precursor of a blood-island, but in all probability such an interpretation is correct. In the narrow prolongation of the yolk-sac to the chorion no angioblastic tissue is recognisable. As already stated, spaces and strands are larger and more numerous in the mesoderm of the chorion where this attachment of the yolk-sac is placed. The endoderm cells of this yolk-sac stalk terminate in the wall of a specially large space containing angioblastic strands. This space with a strand is continued into the slender mesodermic process which replaces the yolk-sac prolongation and terminates in the cavity of the blastocyst. The appearances in this particular area have been described by BRYCE. A further brief description will be necessary but is postponed until similar appearances in other ova have been indicated in the next section of this paper.

#### *Villi.*

In the mesoderm of the villi there is no evidence of commencing vessel formation. Minute spaces or clefts are present without any special condensation of protoplasm or nuclei in their vicinity, and without protoplasmic strands in their lumen. Many of the spaces were



traced in the direction of the chorion, and in no case was communication with a space containing angioblastic tissue in the chorionic mesoderm established; nor do the spaces of themselves form a continuous network in a villus. Probably these spaces in the villi represent the fluid parts of the mesodermic tissue. They may have become slightly exaggerated in the course of preparation of the specimen, as shrinkage of the mesoderm from its trophoblastic covering is not at all common in the villi, while it is seen in places in the wall of the chorion.

Although vascular development is present in the mesoderm of the body-stalk, no evidence of its commencement is found in the prolongation of this on to the amnion. There is no evidence of the commencement of the process in the tissues of the embryonic shield.

#### M'INTYRE EMBRYO.

This specimen was found by the writer in the course of his work as Pathologist at the Royal Samaritan Hospital for Women, Glasgow, in a uterus removed by supravaginal hysterectomy. The uterus was partially opened until the blastocyst projected, was washed in running water and then placed in Kaiserling's formalin and salt solution. The specimen was immersed in the latter fixative less than an hour after operation. The shrinkage of the uterine wall ruptured the decidua capsularis and caused complete separation of the ovum, which came away free when the specimen was next handled.

##### *Measurements—*

External dimensions of chorionic vesicle including villi (after fixation)  $14 \times 13 \times 8$  mm.

Anterior extremity of yolk-sac to posterior extremity of amnion 1.75 mm.

Blastoderm (including primitive streak) length 1.37 mm., greatest breadth 0.5 mm.

Primitive streak 0.32 mm.

Yolk-sac (approximately)  $1.44 \times 1$  mm.  $\times 1$  mm.

Amnion, length 1.28 mm.

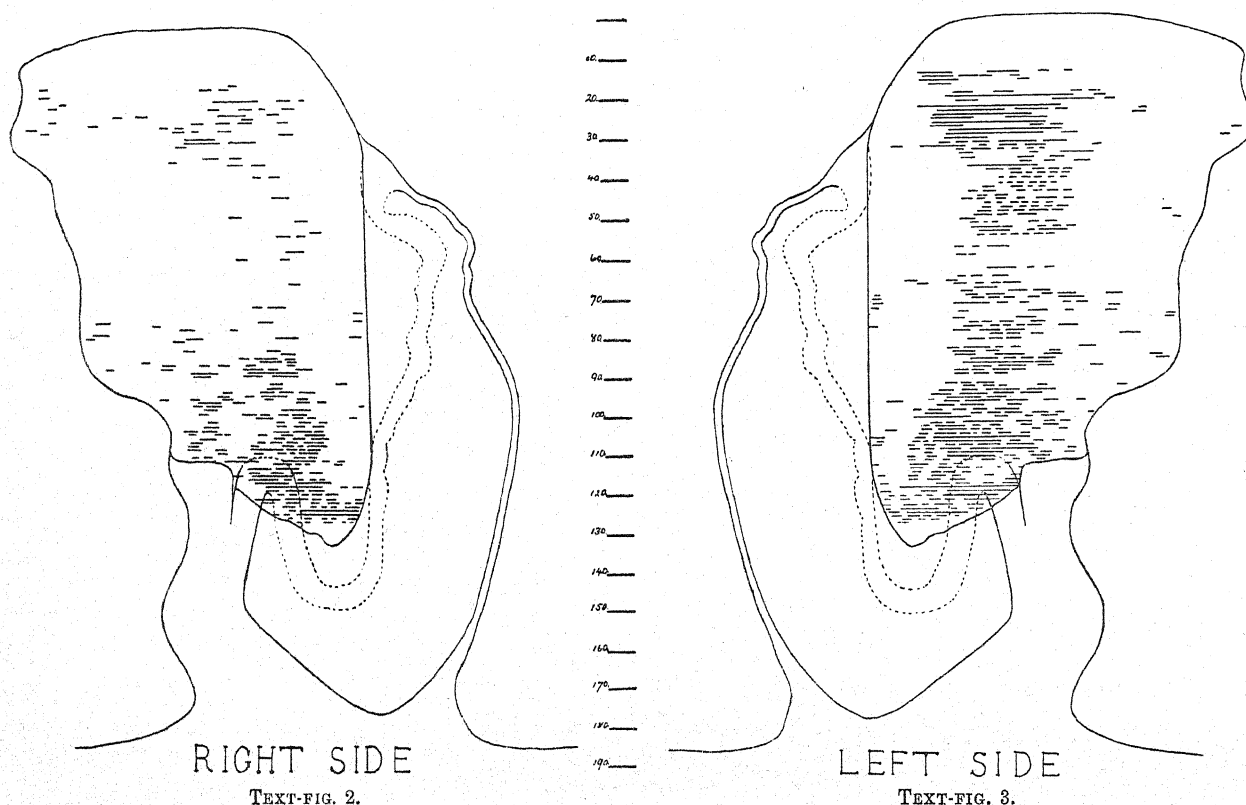
Sections 10 microns thick are numbered from the head end of the embryo to the base of the stalk and pass through the embryonic axis exactly transversely. In this embryo the primitive streak is fully developed. There is a notochordal plate and a neurenteric canal, and the fore-gut has just commenced to close in. The yolk-sac is relatively large and is greater in size than the amnion. The villi show plentiful branching.

##### *Yolk-sac.*

The yolk-sac as yet cannot be said to possess any vessels. Blood-islands are numerous and consist of multi-nucleated protoplasmic masses projecting from the surface of the vesicle. Nowhere is an endothelial-lined lumen with free individual blood-cells found.

As seen in transverse section the endoderm, in the middle line on the ventral aspect of the sac, consists of a single layer of cells of a low columnar type with centrally-situated ovoid nuclei. Traced dorsally to the embryonic area the cells gradually become cuboidal or spheroidal with spherical nuclei. For a short distance before reaching the embryonic shield the cells are flattened out in the line of the yolk-sac wall. This area is the thinnest part, and here there is a longitudinal infolding of the wall. The mesoderm cells have a less regular arrangement and are less constant in size, form, and in shape of nuclei. The intensity of nuclear staining also varies. In the middle line ventrally the mesoderm forms a thicker layer than elsewhere. Towards the embryonic area it is represented by a single layer. There

is a tendency for the mesoderm cells to clump together, and the nuclei in these groups of cells have a radial arrangement relative to the surface. The blood-islands are situated principally in the lateral wall midway between the embryonic area and the ventral aspect (text-figs. 2 and 3). This corresponds to an area just ventral to the thinnest part of the wall. The cephalic end of the yolk-sac for a short distance is totally devoid of blood-islands, but these are seen to appear before the anterior end of the blastoderm is reached. On the left side of the yolk-sac the blood-islands are larger and more numerous than on the right. Again, on both sides they are more plentiful opposite the head end of the embryo and in the area of yolk-sac wall bridging across the tail-fold. Between these two areas they are scanty in



TEXT-FIGS. 2 and 3.—M'INTYRE embryo. The drawing represents a sagittal section of the embryo, amnion, and body-stalk, with superimposed a lateral elevation of the yolk-sac. The blood-islands of the yolk-sac have been plotted in to scale from individual drawings of the sections. The numbers of the sections are indicated. It was not considered necessary to correct the reversal of the view as taken from the sections.

number on the left side and still less numerous on the right. Away from the mid-lateral wall towards the blastoderm margin, or towards the ventral aspect of the yolk-sac, blood-islands are rare and when present are small and in an early stage of formation.

The blood-islands show a variety of forms, and these may be divided for purposes of description into four types which are taken to represent different stages in development.

*Stage 1.*—This form, which is regarded as the earliest evidence of blood-island formation, consists of a hemispherical mass with the central nuclei becoming spherical (Pl. II, fig. 7). The mass projects slightly from the surface of the yolk-sac. The protoplasm possesses no hæmoglobin colouring. This form is taken to represent a stage following on the grouping of mesoderm cells already described. There is no proof that it is the precursor of a blood-island except that the next stage is similar to it, with the addition of hæmoglobin colouring of protoplasm in the centre of the mass.



*Stage 2.*—In this stage (Pl. II, fig. 8), the central nuclei are mostly spherical, have a bold outline, and stain less deeply with hæmalum than the adjacent mesoderm nuclei. In the periphery of the mass showing hæmoglobin colouring one or more deeply stained crescentic nuclei may be seen. These are not constantly present, but when present appear to belong to the central mass rather than to the surrounding protoplasm.

*Stage 3.*—Increase in size of the blood-islands results in definite projection from the surface, and the mass originally hemispherical becomes almost spherical in section. The bulk of it is composed of protoplasm showing hæmoglobin colouring and numerous faintly stained spherical nuclei of regular size (Pl. II, fig. 9). This mass cannot be resolved into individual cells. Surrounding it there is a narrow zone of protoplasm uncoloured by hæmoglobin, with nuclei in a single layer. These nuclei are well spaced and irregular in shape. The protoplasm of this surrounding zone cannot be sharply demarcated from the central mass.

*Stage 4.*—This still more advanced picture (Pl. II, fig. 10) is seen only in a few of the largest blood-islands in the posterior extremity of the yolk-sac at the tail-fold and, therefore, near the commencement of the body-stalk. The central mass now shows the presence of clefts in the protoplasm, dividing it up into irregular masses closely packed together. Some of these masses have attachment to the surface zone. In one or two instances what appeared to be individual cells were seen, but examined alongside neighbouring sections these were decided to be merely narrow terminations of a mass cut transversely so as to show only one nucleus. A greater number of the nuclei of the outer covering now assume a flattened shape.

The blood-islands vary considerably in size, and the size is not related to the intensity of hæmoglobin colouring of the contained protoplasm. Some of the smallest, having only four or five central nuclei, show the protoplasm as intensely coloured as the largest. The blood-islands vary in shape as viewed on the flat, and have an irregular arrangement. So irregular is the distribution that attempts to make a transparency reconstruction of them from the sections were only partially successful. It was possible, however, to appreciate that they do not form a continuously connected network although connection between neighbouring blood-islands is established. At the head end of the vascular zone the blood-islands appear to have their greatest measurement in the axis of the embryo, whereas at the tail end there is a definite tendency for them to be disposed at right angles to the embryonic axis, and here also they are more elongated. In addition, they are not so sharply limited by their outer zone with its elongated nuclei.

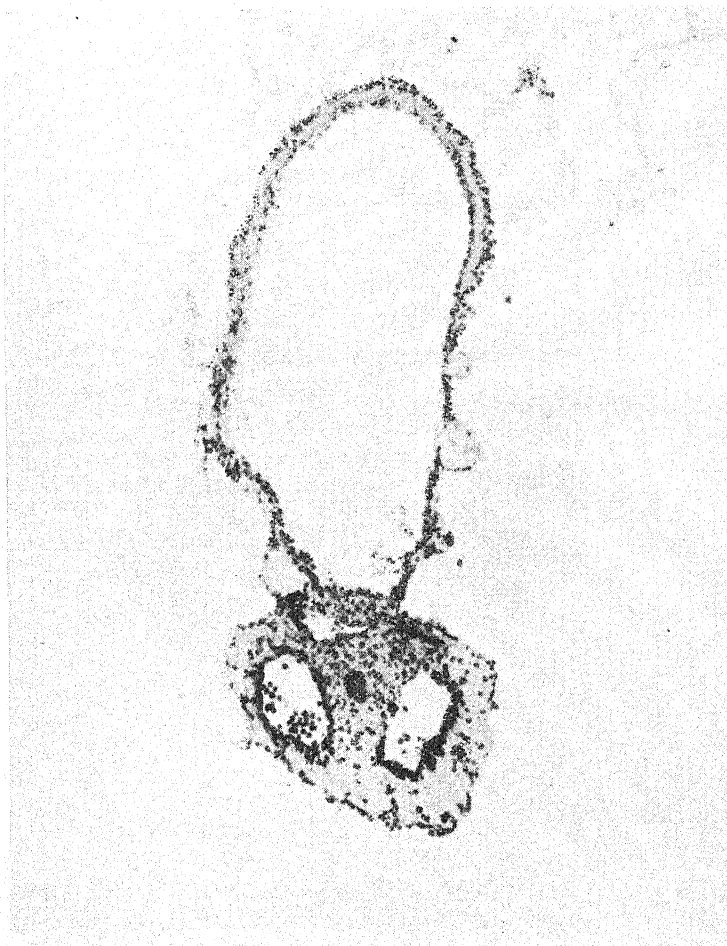
Although there is often difficulty in resolving mesoderm and even endoderm into individual cells, there is no difficulty in differentiating mesoderm and endoderm. This enables one to state that the vascular tissue present is more closely connected to mesoderm than to endoderm.

#### *Body-stalk.*

In section No. 115 the yolk-sac merges into the funnel-shaped diverticulum which becomes the allantoic duct. This is taken to represent the upper limit of the body-stalk. In section No. 190 the stalk merges with the chorion. Its length, therefore, is 0.75 mm. The tail-fold of the embryo reaches as low as section No. 150; the amnion with its lower limit in section No. 175 passes off from the dorsal aspect of the stalk (text-fig. 2). The allantoic duct definitely established in section No. 122 ceases in section No. 166. The stalk in transverse section may be taken as roughly circular in outline, with the allantoic duct situated almost in the centre (text-fig. 4). The stalk increases gradually

in diameter towards the chorion until it breaks up unevenly into strands which turn outwards to join the chorion very obliquely. This gives a very complicated picture in the sections through the lower end of the stalk.

The mesoderm of the stalk consists of a finely reticulated protoplasm which stains faintly with the basic stain employed. The nuclei are vesicular, are lightly stained with hæmalum, are of fairly regular size, and are slightly ovoid or short rod-shaped. This



TEXT-FIG. 4.—M'INTYRE embryo. Photomicrograph by Professor J. H. TEACHER of a section of the body-stalk. The prolongation of the amnion also appears, and is seen passing off from the dorsal aspect. The allantoic duct can be recognised about the centre of the stalk. On either side of it an umbilical artery is present; behind it on one side a venous space is seen and on the other side an angioblastic mass (the dark elongated area). In the mesoderm of the amnion wall the "blisters" referred to in the text are shown.  $\times 120$ . Section No. 154. See text-fig. 2.

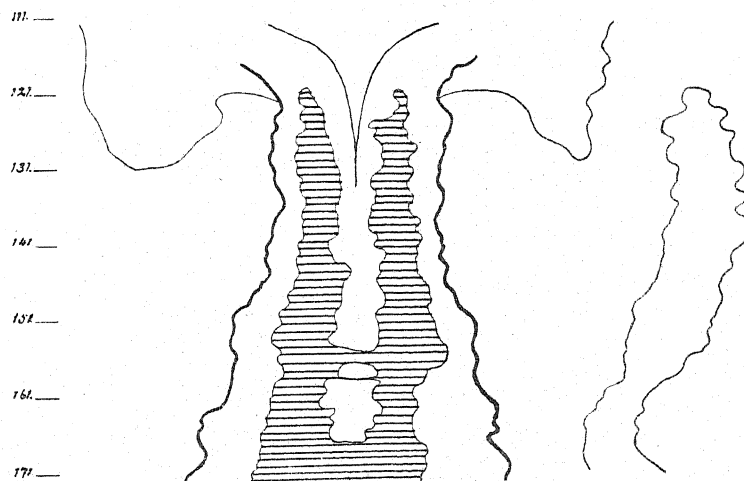
tissue cannot be resolved into individual cells, nor is there any sharp condensation of protoplasm around the nuclei. A mesothelial layer is present (Pl. III, fig. 11). It is most complete at the level of the middle of the stalk, where it consists of a thin film of protoplasm which has taken up the eosin stain and a single layer of round nuclei smaller than and more deeply stained than the ordinary mesoderm nuclei. The nuclei are irregularly spaced; sometimes wide intervals exist between two nuclei. This covering is incomplete at both extremities of the stalk.

The presence of two large vessels (the umbilical arteries) containing free cells and of



approximately equal size forms the most striking feature of the stalk (text-fig. 5). These are situated one on either side of the allantoic duct at the embryonic extremity. Both have a wide lumen. They commence in section No. 121, and as they pass towards the chorion they increase in size and gradually come to lie anterior to the allantoic duct. In section No. 156 they connect across in front of this duct by a narrow open channel; in section No. 159 they connect by a solid strand; in section No. 168 they unite to form a single large vessel which in section No. 180 again splits up into two main branches running to the chorion.

The vessel walls consist of a condensation of nuclei and protoplasm. The nuclei are of shape similar to the ordinary mesoderm nuclei, and lie one, two, or three deep in the wall of the vessel. This contrasts with the surrounding mesoderm, which is specially scanty in nuclei in the ventral half of the stalk through which the vessels run. The condensation of protoplasm corresponds to the nuclear zone and takes up the eosin stain.



TEXT-FIG. 5.—M'INTYRE embryo. Front elevation of the body-stalk, showing the two arteries present, and a lateral view of the left vessel assembled from drawings of individual sections.

Elongated nuclei which might be regarded as belonging to endothelium are present only at wide intervals. The lumen contains free nucleated blood-cells. These are rounded or polygonal and have a relatively large amount of protoplasm which shows unmistakable hæmoglobin colouring. The nuclei are very regularly spherical and are situated centrally. They vary greatly in intensity of staining. Some stain so faintly that the presence of a nucleus is made out only with difficulty. In others the nucleus stains very deeply. Mitotic figures are seen, and the presence of two nuclei, one sometimes larger than the other, in a single cell is not uncommon. No syncytial masses are seen in the vessels, but now and then blood-cells lie closely applied to the wall. In the latter, however, direct protoplasmic continuity does not exist.

Occasionally a V-shaped depression or cleft in the wall of the vessel passes outwards towards a small mass of angioblastic tissue. Such masses are not specially common in association with the vessels at present being described. They resemble the cells within the vessels, and are sharply demarcated from the surrounding unaltered mesoderm.

Sometimes the vessels appear to communicate with the mesothelium by a cleft or depression in the vessel wall passing towards another cleft on the surface of the stalk, the

interval being bridged across by a solid strand. This is not frequently noted nor is it a conspicuous feature. Complete open communication is not found.

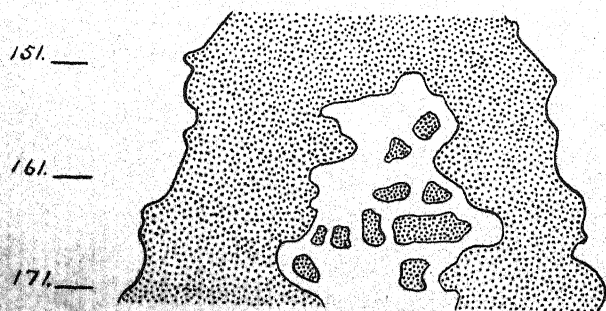
Traced towards the embryo the two vessels end blindly, and there is no connection established with the angioblastic tissue of the yolk-sac, neither by open channels nor by solid strands. In the stalk above the termination of the vessels there is angioblastic tissue, but this is less in amount than at any other level of the stalk.

Although in the mid-line the yolk-sac is replaced by its posterior diverticulum in section No. 115, the lateral walls are continued downwards to bridge across the tail-fold of the embryo to section No. 131. The amnion is now interposed between the yolk-sac and the body-stalk (text-fig. 2). The possibility of angioblastic connection between the stalk and this part of the yolk-sac wall rich in blood-islands by way of the amnion wall was excluded. Several small isolated masses of angioblastic tissue were encountered in the amnion mesoderm here, but only close to the stalk, and they might be regarded as belonging to the latter.

Another picture of vascular development is found in the dorsal part of the stalk and would appear to be unconnected with that already described. At the junction of the embryonic and middle thirds of the stalk, behind the allantoic duct and frequently situated near the angle between the body-stalk and the amnion on either side, angioblastic masses are seen. Some of these have an appearance rather like the blood-islands of the yolk-sac. They lie just under the mesothelium and have a few crescentic nuclei disposed around them—the central mass showing hæmoglobin-coloured protoplasm. They form, however, no projection on the surface. Passing towards the chorion this gives place to larger irregular masses of the same structure, only differing in shape, running directly dorsal to the allantoic duct. About the middle of the body-stalk these become smaller in size, are diffusely distributed, and sometimes show connection by clefts with a network of spaces which has appeared at this level. The walls of the spaces have the same appearance as that of the vessels already described, except that condensation of nuclei is less marked, endothelium-like nuclei are less frequently seen, and the protoplasm in the wall stains less deeply with eosin. The spaces connect up with one another behind the allantoic duct in an irregular manner. In transverse section the lumen is often stellate. Numerous V-shaped depressions pass outwards to end in solid processes which sometimes run to isolated angioblastic masses. Two clefts passing outwards from a space may converge and almost isolate a mass, as

it were, in the lumen. This mass has the same structure as the wall of the space elsewhere. There is no hæmoglobin colouring of the protoplasm nor other indication that it will be any more closely concerned in the production of endothelium or blood-cells than the other parts of the wall.

The main channels of this network are represented in the diagram as they exist in the middle third of the stalk (text-fig. 6). Nearer to the chorion they become smaller in size, more numerous, and more complicated



TEXT-FIG. 6.—M'INTYRE embryo. The plexus of spaces in the dorsal region of the stalk in the same view as text-fig. 5.

in arrangement. They can be traced to the mesoderm of the chorion. At this end of the body-stalk they cannot be traced as continuously connected. Some of them establish connection by solid processes with the walls of vascular channels in the chorion which contain



undoubted blood-cells. Although this network of spaces contains no blood-cells, it is certainly the commencement of a capillary network, the future umbilical veins.

Throughout the examination of this area particular attention was directed to the relationship of the angioblastic tissue to the mesothelium. Mention of this has already been made in connection with the umbilical arteries. In one instance what is almost certainly a connection between a well-formed angioblastic mass and a funnel-shaped depression of the mesothelium was found (Pl. III, fig. 11). This mass, which can be traced through twelve sections, in one part of its course may be regarded as a vessel. At two points it appears to have connection with the mesothelium, while at another level it connects by a solid strand with the network of spaces behind the allantoic duct.

### *Chorion.*

It will be necessary to refer to the structure of the mesoderm before describing the vascular picture. In the vicinity of the base of the body-stalk the mesoderm has a loose arrangement. It cannot be definitely resolved into individual cells, although here, unlike the mesoderm of the stalk, there is evidence of some concentration of protoplasm often in the form of a spindle around the nuclei. The nuclei vary in shape from short ovoid to rod-form with blunt extremities. They lie principally with their long axes parallel to the chorion. Around the base of the stalk one frequently finds the mesoderm marked off into two layers by a very loose arrangement of the tissues in its middle. Under such circumstances, the mesoderm lining consists of one sheet clothing the trophoblast and another lining the blastocyst cavity. The latter contains the largest chorionic vessels seen, and would appear to be formed as a result of these large vessels leaving the chorion to pass into the stalk. Away from the attachment of the stalk the mesoderm of the chorion is a thinner, more compact layer, and gives indication of the presence of wavy fibrillæ. The nuclei are relatively less numerous and approach nearer in appearance to adult fibrous tissue nuclei. The inner surface of the mesoderm near the body-stalk has, in areas, fine irregular protoplasmic strands streaming off into the cavity of the blastocyst. A mesothelium as such is not recognisable.

Vessels and solid angioblastic strands are present in the chorion, but only in an area limited to the vicinity of the base of the body-stalk. In this area they are quite numerous.

The earliest stage of vessel formation recognisable consists of a thin, solid strand of protoplasm staining rather deeply with eosin and partially, but not completely, marked off from its surroundings. It is never situated in a space as described for the angioblastic strands in the chorion of the T. B. No. 2 ovum. Three or four rod-shaped nuclei are arranged in a single row in the protoplasm. The next stage is the appearance of a nucleated hæmoglobin-coloured cell in the strand. This cell is sharply demarcated and is distinctly a free cell. It lies in a space provided for it in the protoplasm of the strand, sometimes at its middle, sometimes at one extremity. This cell may be as great in thickness as the strand which contains it, and the protoplasm of the strand where it passes on either side to enclose it is thinned out and may be readily overlooked by the observer.

More commonly, the strand, before the appearance of frank hæmoglobin colouring in the cell, contains a double or treble row of elongated nuclei (Pl. III, fig. 12). Next, several hæmoglobin-coloured cells appear in a row and are situated in the middle of the strand (Pl. III, figs. 13 and 14). These are sharply marked off from their surroundings and from one another, and the ends of the cells where in contact are flattened so that the

cells are frequently square in shape, the other two sides being flattened against the walls of the space in which they lie. The appearances are such as to suggest almost that the cells are under compression.

These strands may be isolated or may establish protoplasmic connection with others of any stage in development. Intermediate stages are seen right up to the largest vessels present. Some of the latter have a lumen almost equal in size to that of the vessels in the stalk. Their walls consist of a condensation of protoplasm with numerous rod-shaped nuclei disposed parallel to the lumen. The structure of the vessel wall, apart from its richness in eosin staining and the regular arrangement of the nuclei, has no special feature to distinguish it from the surrounding mesoderm. There is not as yet a lining to be compared with adult endothelium. In these larger vessels the lumen contains free nucleated blood corpuscles, sometimes of irregular shape but the majority spherical. They differ in no way in appearance from those in the vessels of the body-stalk. The angioblastic tissue present tends to run parallel to the chorionic membrane, and takes part in the formation of a network. The more mature vessels in the vicinity of the attachment of the stalk communicate together in a complicated manner. The earliest representations of vessels may connect up over limited areas either by solid strands or in part by open channels. Angioblastic strands are seen isolated, and these sometimes already possess cells in which hæmoglobin colouring of the protoplasm is beyond doubt.

No angioblastic tissue is found directly in contact with the chorionic epithelium; only a few of the earliest strands are seen near the epithelial layer. As already stated, the vascular development is specially prominent on the inner (cavity) aspect of the chorionic mesoderm. This, along with the short distance in which a vessel with a wide lumen may be replaced by a solid strand, forms two striking features of vascular development in this area.

Special attention was directed to the vascular connection between the body-stalk and the chorion. Tracing the rudiments of the umbilical arteries from their common trunk at the lower extremity of text-figure 5, section No. 172, this single vessel divides into two. In section No. 180 the two branches passing away from one another become continuous with the network of vessels in the chorion. The arterio-vascular system in the body-stalk and chorion thus communicate by open channel. The venous plexus of spaces, at the junction of the body-stalk and the chorion, establishes connection with solid angioblastic strands which are specially numerous in the vicinity of its termination, and by way of some of these with a few of the smallest vessels in the chorion. A connection by open channel was not made out. As far as could be gathered by tracing vessels and angioblastic strands, no connection exists either directly in the body-stalk or indirectly in the chorion between the two sets of vessels in the stalk, viz. the two arteries on the one hand and the venous plexus in the dorsal part of the stalk on the other.

#### *Villi.*

The villi are well formed, are of considerable length, and show intricate branching. The mesoderm of the villi differs from that of the chorionic membrane in that there is no concentration of protoplasm around the nuclei. The protoplasm, which is of finely granular structure with a very fine network of fibrillæ, stains faintly with the basic stain. It, therefore, resembles the mesoderm of the body-stalk in its staining reaction. The nuclei, on the whole, are situated wide apart and are not equidistant from one another, but are some-

times grouped together in collections of three or four. The blood-vascular development in the villi has reached a critical stage.

There are, in the first instance, in the villi in the vicinity of the base of the stalk, angioblastic strands consisting of a single row of nuclei usually, but sometimes of a double row, surrounded by protoplasm which stains deeply with eosin. These, therefore, stand out sharply in contrast to the general mesoderm of the villus which is faintly stained with hæmalum. A detailed description is unnecessary, as they have the same appearance as strands of similar dimensions in the chorion. In several the origin of hæmoglobin cell from angioblastic strand is seen. In the vast majority of instances these strands run in the middle of the mesoderm in the axis of the villus. Exceptionally a short strand may run obliquely until it reaches near to the epithelial covering but never comes in contact with it. There is no space separating the strands from the mesoderm.

Such angioblastic strands as have now been described exist as already stated in a very restricted area at the base of the body-stalk. Elsewhere the villi show no evidence of commencing blood-vessel formation. Even in the area where these strands are present, the great majority of villi as yet show no indication of the commencement of the process.

The strands may lie in the base of the villus or half way between the two extremities. In the few instances where a strand is seen near the distal extremity, it stops a considerable way short of the tip of the villus. One angioblastic strand in the base of a villus was traced back into the chorion and eventually into what was sufficiently well developed to be termed a vessel.

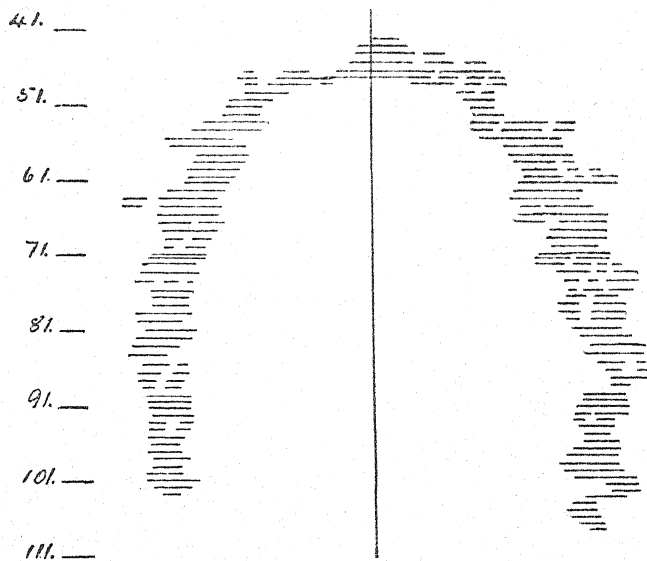
Numerous strands, at all levels in villi, traced backwards are found to terminate

short of the chorion, and, therefore, have no connection with the vascular system therein. In fact, in examining a villus, one may encounter two angioblastic strands at different levels unconnected with one another or with the chorion.

In only two cases was a villus found to contain free nucleated cells showing a hæmoglobin reaction, or, in other words, a "vessel." In one case the vessel established connection with a vessel of the chorion. In the other its proximal extremity terminated at the base of the villus in a solid strand which did not establish connection with any of the vascular elements in the chorion.

#### *Embryonic Rudiment.*

The pericardial cœlom is present in the form of a U-shaped space (text-fig. 7). The limbs of the "U" extend backwards in the mesoderm near the lateral borders of the embryo. Here the mesoderm consists of a double layer of cells, and the cavity is formed by separation of this double layer. When formed, therefore, the walls of the cavity dorsally and ventrally consist of mesoderm with a single row of nuclei (text-fig. 8).

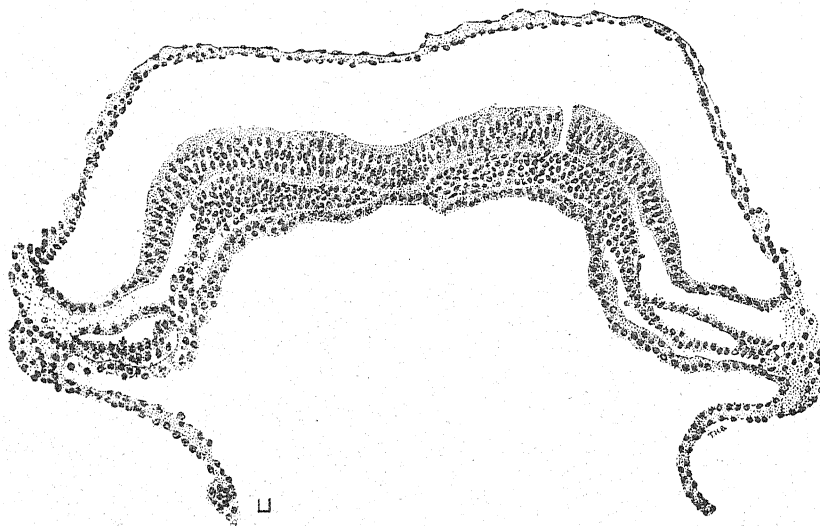


TEXT-FIG. 7.—M'INTYRE embryo. The pericardial cœlom viewed antero-posteriorly. Graph-reconstruction from individual sections.



Here and there the roof and floor come into apposition with one another for a short distance dividing the lumen into two. On the right side the canal extends back to section No. 107, on the left to section No. 102.

At the anterior extremity of the embryonic area they unite with one another to complete the formation of the "U." This portion of the "U" is bent slightly downwards conforming to the shape of the embryo. If the sections are examined from the head end backwards this union in front appears first in section No. 42, which is also the first section in which the cavity of the amnion is apparent.



TEXT-FIG. 8.—M'INTYRE embryo. Section No. 65. See text-figs. 2 and 7. The pericardial coelom is seen on either side.  
(By permission of Professor T. H. BRYCE.)

The entire embryo was carefully examined, especially the floor of the pericardial cavity, and nowhere were any changes found which could be regarded as evidence of early blood or vascular development. Nothing which could represent the commencing formation of the endothelial heart-tubes was recognised.

#### NOTES ON VASCULAR DEVELOPMENT IN EARLY EMBRYOS.

Having completed the description of these two specimens, and before developing any general conclusions, it may not be amiss to supply brief notes of the vascular development in other early embryos. It will not be necessary to analyse the points in every specimen which has been described. It will suffice if I restrict my analysis to *Bryce's Selected List* with the addition of three others, viz. MEYER'S, TRIEPEL'S, and INGALLS' (1920) specimens. BRYCE's list is an approximation to a sequence in respect of differentiation and the order is maintained. MEYER's ovum I have placed between T. B. No. 2 and STRAHL-BENEKE'S. TRIEPEL'S and INGALLS' (1920) ova are included after GRAF v. SPEE'S "Gle."

The source of each specimen is indicated and, where available, a measurement of the embryo and of the blastocyst are given. Very short notes of the two specimens just described are inserted to make the list complete.

J. W. MILLER (1913).

Curettage. Embryonic rudiment solid. Blastocyst 0.44 mm. There is no extra-embryonic coelom. There are no villi. There is no indication of the commencement of vascular development.

## TEACHER-BRYCE No. 1 (1908).

Abortion. Embryo about .15 mm. Blastocyst  $.77 \times .63 \times .52$  mm. There is no extra-embryonic coelom. There are no villi. There is no indication of the commencement of vascular development. I have had the opportunity of examining the specimen and I agree with this finding. BREMER, also, came to the same conclusion after examination of the sections.

## V. MOLLENDORFF (SCH.) (1921).

Abortion. Embryonic knot. .17 mm. Blastocyst .26 mm. There is no extra-embryonic coelom. There are no villi. There is no indication of the commencement of vascular development.

## LINZENMEIER (1914).

Vaginal hysterectomy. Embryonic anlage .21 mm. Blastocyst  $.75 \times .615 \times .525$  mm. The extra-embryonic coelom is present. Villi have formed and in these as in the mesoderm in general there is no trace of the commencement of vessel formation. The body-stalk has not yet assumed its characteristic appearance, the embryo lying in a collection of mesoderm on the wall of the blastocyst. The anlage of the allantois is described as lined with epithelium coloured like red-blood corpuscles. It is of interest to note that the cells of the allantoic duct in the M'INTYRE embryo have a somewhat similar appearance; so much so that this structure might readily be mistaken for angioblastic tissue. No further note of vascular development is made.

## PETERS (1899).

Suicide autopsy. Embryo .19 mm. Blastocyst  $1.6 \times .8 \times .9$  mm. The extra-embryonic coelom is present. The villi have a mesodermic core. A body-stalk can hardly be said to exist. In the model made by KEIBEL from drawings by SELENKA, the external surface of the yolk-sac appeared uneven, but it could not be decided if these represented the anlagen of vessels.

## JUNG (1908).

Curettage. Embryonic anlage about .25 mm. Blastocyst  $2.5 \times 2.2$  mm. All trace of vessels is absent from the chorion and villi. In the body-stalk there are present collections of cells with a lumen in their middle. The lumina have no contents resembling blood corpuscles. He hesitates to decide whether or not these are the first vessel anlagen. Vessels are not recognisable in the embryonic mass.

## SCHLAGENHAUFER AND VEROCAY (1916).

Suicide autopsy. Embryonic shield .24 mm. Blastocyst  $2 \times 1.6 \times 1$  mm. A well-defined body-stalk is present. In the mesoderm of the yolk-sac are thickenings which are regarded as the anlagen of blood-islands. The commencement of vascular development is not noted in the body-stalk, chorion, or villi.

## FETZER (1910).

Curettage. Embryonic shield .23 mm. Blastocyst  $1.6 \times .9$  mm. The villi are vessel free. There is no mention of vascular development in the chorion. No vessel anlagen are present in the body-stalk or in the amnion wall. The mesoderm of the yolk-sac shows numerous projections but there is nothing found which could be called a vessel anlage. A process passes out from the yolk-sac to end free and without attachment to the chorionic wall.

## V. MOLLENDORFF (OP.) (1921).

Hysterectomy. Chorionic vesicle  $2.25 \times 2 \times 2.5$  mm. In one instance in the embryonic shield a collection of mesoderm cells is found near the entoderm. Similar cell groups are found in the mesoderm of the yolk-sac. He does not decide definitely that these are concerned in the formation of blood or of vessels. In the chorion he finds here and there channels lined with flattened cells. These are pronounced to be vessels. Their cavities do not yet connect up to form a continuous system. There is apparently no vascular development in the body-stalk or in the villi.

## HERZOG (1909).

Autopsy. Embryonic shield 1.54 mm. Blastocyst  $2.3 \times .8 \times 1.2$  mm. The villi consist of projections without dichotomous branching. At the junction of the yolk-sac and body-stalk mesoderm there are found some solid and some open circular masses of mesoderm cells. These formations are taken to represent the earliest "anlage" of the yolk-sac blood-vessels. BREMER regards HERZOG's interpretations of these cellular rings as incorrect. The mesoderm of the chorion and of the villi do not yet show any trace of blood-vessels. There is no mention of blood-vessel development elsewhere on the yolk-sac or in body-stalk or in the embryo itself.

## TEACHER-BRYCE No. 2 (1924-26).

Autopsy (acute rheumatism). Blastoderm .2 mm. Blastocyst cavity  $2.8 \times 2.6 \times 2.25$  mm. Angioblastic strands are found in spaces in the chorionic mesoderm. These are most plentiful around the base of the body-stalk and are not continuously connected. The body-stalk contains similar but larger strands and spaces at its base. Nearer the embryo several spaces contain collections of cells having the appearances of primitive blood-cells. What is probably the commencement of blood-island formation is found in the wall of the yolk-sac. No angioblastic formation is recognised in the embryonic shield or in the villi.

## MEYER (P. M. 1923) (1924).

Curettage. Embryonic shield .41 mm. Chorionic cavity  $2.6 \times 2.1 \times 2.72$  mm. No indication of vascular development is found in the mesoderm of the chorion or in that of the villi. The yolk-sac possesses blood-islands which do not communicate with one another and are furthest developed over the ventral aspect. A blood-island consists of a collection of cells between the yolk-sac entoderm and the mesoderm coat with a narrow connection to the latter. He finds in the body-stalk dorsal to the allantoic duct a collection of cells which he regards as the first anlage of the umbilical artery. There is no mention of vascular development in the embryonic shield. The yolk-sac possesses a long process which passes across the blastocyst cavity to terminate in a vesicle in the chorionic mesoderm at the implantation pole. The yolk-sac prolongation contains no blood-islands. The vesicle he regards as lined on the outer (trophoblast) side by mesoderm, on the inner (towards the chorionic cavity) by entoderm. This is covered by mesoderm which separates it from the lumen of the chorionic cavity and between the two layers he figures a blood-vessel anlage (fig. 12, p. 59). One is unable to recognise the entoderm lining of the vesicle from the figure, otherwise, apart from the absence of strands in the lumen, the vesicle has the appearance of the spaces in the mesoderm at the attachment of the yolk-sac duct in the Teacher-Bryce ovum No. 2. Blood-islands, he points out, are found nowhere away from entoderm, and he takes this as indicative that the blood-islands have some relation to entoderm.

## STRAHL-BENEKE (1910).

Curettage. Embryonic shield .75 mm. Blastocyst  $3.8 \times 2.2 \times 1.2$  mm. In this ovum on the under surface of the yolk-sac there are thickenings of mesoderm containing cell masses which are regarded as the forerunners of vessels, but these have not yet acquired the definite characters of vessels. Sharply defined spaces in the mesodermic envelope of the embryonic body and specially marked on the yolk-sac side are referred to as "like capillary vessels." These spaces do not form a closed tube system and are empty except in one place where free cells are present. These cells, however, show no hæmoglobin colouring of their protoplasm. BENEKE thinks he can recognise similar spaces in the mesoderm of the Teacher-Bryce ovum No. 1 in the photograph (Pl. ii) reproduced by the authors. In the mesoderm of the chorion of the STRAHL-BENEKE ovum spaces similar to these described in the embryonic sections are present and are referred to as having the appearance of empty endothelial tubes. The authors' fig. 1, however, shows mesoderm of the chorion which in the description of the figure is stated to be vessel-free. The villi have a mesodermic core in which there are no vessels. This ovum has a prolongation of the yolk-sac which runs to the chorionic wall. There is no note of vascular development in this structure, nor does there appear to be any particular development of spaces in the mesoderm of the chorion where this structure reaches it.



## GRAF VON SPEE (V. H.) (1896).

Abortion. Embryonic shield 37 mm. Blastocyst 4 mm. Spaces in the chorionic mesoderm and in the body-stalk have no visible content; neither blood nor endothelial cells are found. The yolk-sac wall has irregular protuberances of the mesoderm. Corresponding to these are blood-islands situated between mesoderm and entoderm. The youngest stage of blood-island lies nearest to the embryonic disc. The formation of blood-islands is noted as extending nearer to the embryonic disc than in his older embryo "Gle." EVANS, in KEIBEL and MALL'S *Manual of Human Embryology*, states that some of the vascular anlagen of the yolk-sac of this embryo show evident differentiation into endothelium and blood-cells. Also, that in the body-stalk and chorion there are, as GRAF SPEE has described, "highly characteristic strands of spindle cells." This he thinks suggestive of endothelium, although there is no blood-cell formation.

## LEWIS (MINOT) (1912).

In the yolk-sac wall among the mesodermic cells are vessels with a true endothelial lining and containing nucleated blood corpuscles. Sometimes a corpuscle is closely applied to the endothelium as if arising from it. The vessels of the yolk-sac do not pass into the body-stalk, which contains numerous vessels. There are spaces in the chorion which are regarded as vessels. "Frequently these contain strands of darkly staining cells suggesting collapsed endothelium." There are no vessels in the embryo proper. It is not definitely stated that the vessels in the body-stalk are not in continuity with the spaces in the chorion, but this may be inferred.

## STREETER (MATEER) (1920).

Hysterectomy. Embryonic plate 1 mm. Blastocyst  $6.1 \times 5.6 \times 2.5$  mm. Evidence of blood-vessel formation is present in all parts of the chorion. All stages from simple multinucleated protoplasmic strands to completed endothelial tubes are seen. In the villi the stage of development is similar to that in the chorion except that the vessels appear to be more numerous, although a great many villi, as a rule the smaller ones, show no sign of vessel formation. Embryonic blood-cells are recognised. In the body-stalk vascularisation has occurred to the same degree as in the chorion, and as in the latter vessels are mostly empty. Blood-vessel formation is also recognised over the greater part of the parietal mesoderm covering the amnion. Angiogenesis in the yolk-sac is limited to the caudo-ventral half, and is represented by clumps of cells up to completely formed endothelial tubes. In this process of vessel formation in the yolk-sac relatively few complete cells (blood corpuscles) result, and none of these as yet show evidence of the presence of hæmoglobin. The process does not appear to have commenced in the embryo proper. The continuity or otherwise of the vessel-forming tissues in the different areas is not definitely stated.

## DEBEYRE (1912).

Hysterectomy. Embryonic shield 85 mm. Blastocyst  $5.6 \times 2.1$  mm. There is no intra-embryonic coelom. The yolk-sac possesses blood-islands over the distal pole. These vary from a solid group of cells arranged concentrically to irregular festoons containing cells compactly arranged. Apparently the cells show no hæmoglobin colouring. The islands do not form a network. In the body-stalk blood-islands are present. Two of these are specially large and one of them describes a third of a circle spirally round the allantois. In the embryo there is a cellular collection which DEBEYRE thinks may be the first cardiac formation. In the villi occasionally a lumen is seen but without endothelial lining. He states that if these are vessels they represent a very early stage of development. Vessels are present in the chorion. The question of continuity of vessel-forming tissue in the different areas is not discussed.

## THOMPSON AND BRASH (1923).

Curettage. Embryonic shield including caudal fold 9 mm. Chorionic vesicle  $10 \times 7.5 \times 4$  mm. There is no intra-embryonic coelom. Blood-islands are found on the ventral aspect of the yolk-sac and appear to be more advanced in development in the cranial half. All stages from small clumps of cells to

completely formed vessels containing developing blood-cells are encountered. The description and figure would suggest that the blood-cells arise from entoderm, while the endothelium arises in the vicinity of mesoderm, although the writers do not arrive at any definite conclusion with regard to this. The doubtful presence of angioblastic tissue in the body-stalk is noted, otherwise there is no further evidence of vascular development in this specimen.

ROSSENBECK (PEH. I) (1923).

Hysterectomy. Embryonic shield 1.4 mm. In this specimen the presence of the anlage of the aorta is suggested but not definitely affirmed. The mesoderm of the amnion contains endothelial-lined spaces not continuously connected. Two strands run from the amnion to the chorionic mesoderm, one traversing the body-stalk. Both end in connection with vessel anlagen in the chorion. The picture of angiogenesis in the yolk-sac is stated to be the same as in STREETER's (Mateer ovum). In the body-stalk at its caudal end, two endothelial-lined lumina—vessel anlagen—appear. These traced caudally end in an unpaired vessel anlage which lies near the ventral surface of the stalk, and which finally divides and passes into numerous but not continuously connected vessel anlagen in the chorionic mesoderm. Vascular development in the villi is not mentioned.

STRAHL (1916).

No history. Embryonic anlage .7 mm. Chorionic vesicle with villi about 10 mm. diameter. There is no mention of vascular development in the embryonic shield or chorion. Vessel anlagen are not recognised in the body-stalk or villi. Vessel anlagen are present as thickenings in the mesoderm of the yolk-sac wall. Cells, free in the lumen of the yolk-sac, are regarded as nucleated red-blood corpuscles.

GROSSER (1913).

Abortion (after operation.) Embryonic shield including primitive streak .67 mm. Chorionic cavity 6 to 8 mm. across. Vessels are absent from the embryonic area. The yolk-sac shows blood-islands on the distal pole. Blood corpuscles are recognised by their intensive staining, and the lumina of the blood-islands possess an endothelial lining. The blood-islands are already connected together in some parts. In the body-stalk and chorion there are empty cleft-like spaces resembling vessels and lined by fairly irregular endothelium. At a single place in the body-stalk there is a true blood-island. Vascularisation of the villi is not mentioned. A mesoderm strand passing from the yolk-sac right across the cavity of the blastocyst to the chorion shows the presence of entodermal cysts. In the wall of one of the larger cysts blood-islands are present.

INGALLS (1918).

Abortion. Blastoderm 2 mm. Ovum external measurements  $9.1 \times 8.2 \times 6$  mm. In the embryo there are no vessels or blood-cells. Spaces present "might stand in some relation to the future pericardial coelom." Over the fundus of the yolk-sac there is extensive formation of blood-cells and blood-vessels. The body-stalk contains numerous vessels filled with nucleated red cells. There are a few "funnel" ingrowths of mesothelium, but connection of these with "unlined" spaces and angioblast cords, which are also present, is not specially evident. Vessels and solid strands are present in the chorion and villi, and are most frequent near the attachment of the body-stalk. The question of continuity of vascular tissue in the body-stalk, chorion, and villi is not entered into, but it is definitely stated that the vessels in the stalk are not in connection with the vascular tissue of the yolk-sac.

FRASSI (1907-08).

Vaginal hysterectomy. Embryonic shield 1.17 mm. Blastocyst cavity  $9.4 \times 3.2$  mm. There is apparently no vascular development in the embryonic area. The yolk-sac possesses early blood and blood-vessel anlagen which are situated between mesoderm and endoderm (fig. 16, 1908). As far as I can make out from fig. 16 (1908), the cells in the centres of the blood-islands are individual cells, and the limiting cells approach more nearly to endothelium than is the case in the MINTYRE ovum. Blood-vessels are present in the body-stalk and, according to GROSSER, one of these contains blood-cells, the remainder being

empty. Vessel anlagen in the chorionic mesoderm are only recognised with certainty near the insertion of the body-stalk, and two of these at the base of the body-stalk (fig. 17, 1908) show the presence of free cells. Vessel anlagen are not found in the villi. Fig. 15 (1908) shows a small cyst on the wall of the yolk-sac in association with "the anlage of a blood-vessel with blood." The epithelium of this cyst is similar to the coelomic epithelium where it passes over the blood-vessel anlagen. JUNG, referring to this ovum in the description of his own ovum, implies that all trace of vessels is absent from the chorion.

M'INTYRE (1924-26).

Hysterectomy. Blastoderm (including primitive streak) 1.37 mm. Chorionic vesicle external dimensions including villi (after fixation)  $14 \times 13 \times 8$  mm. Blood-islands are seen in the lateral walls of the yolk-sac. They are more numerous on the left than on the right side. They do not form a continuously connected network. None of these structures has reached a stage in development which would permit one to call it a "vessel." The body-stalk possesses two large vessels regarded as the umbilical arteries, and dorsal to these a venous plexus of spaces. Neither of these systems is in connection with the blood-islands of the yolk-sac, nor do they appear to communicate with one another, but both can be traced into the chorion. In addition to the above elements, small solid angioblastic masses, some not unlike the blood-islands of the yolk-sac, are found scattered throughout. All stages of vessel formation are seen in the chorionic mesoderm in an area around the base of the body-stalk, and are restricted to this area. The commencement of vascularisation of the villi is noted only in the villi belonging to the same area. In only two villi could a "vessel" be said to be present. Angioblastic tissue is found isolated in the mesoderm of the villi. In the embryo no evidence of the commencement of formation of the heart or of vessels was found. The pericardial coelom has the form of a "U"-shaped tube.

ETERNOD (VULLIET) (1894).

Abortion. Embryo 1.3 mm. Blastocyst cavity  $6 \times 4.8 \times 3.6$  mm. There is in this embryo a horse-shoe shaped heart of symmetrical outline giving rise to two primitive aortæ (with three or four aortic arches) which are continued into two umbilical arteries in the body-stalk, and presumably through these into vessels in the chorion. The villi are commencing to become vascularised. On the venous side, veins run from the chorion to unite in the body-stalk to form the future umbilical vein; this divides into two, the branches running forward in the mesoderm of the yolk-sac on either side to the primitive heart. Circulation is thus established. Posteriorly a venous loop is formed around the allantoic canal. There is evidence of vessel formation in the amnion wall, and some of these elements are already canalised. In addition to the veins mentioned above, the yolk-sac possesses blood-islands and vessels in which the lumen is already established.

GRAF VON SPEE (GLE.) (1889).

Abortion. Embryonic shield 1.54 mm. Internal dimensions of chorion  $7.5 \times 8$  mm. No vessel formation nor commencement of development of the heart is found in this embryo. A space is present in the embryonic mesoderm. Blood anlagen are present exclusively in the wall of the yolk-sac. The mesoderm of the body-stalk and yolk-sac is rich in spaces having a smooth lining of low cells like embryonic endothelium. In the yolk-sac, cell strands lying between mesoderm and entoderm are more closely connected with the mesoderm.

EVANS, in *Keibel and Mall*, reproduces a drawing of a section in which the above-mentioned space in the embryonic mesoderm is shown, and he regards it as the pericardial cavity. In the same section the anlage of the cardiac endothelium is seen. Vascular anlagen are recognised in the embryonic area, and these can be traced into the vessels in the body-stalk—the anlagen of the umbilical arteries. He also recognises the presence of vessels in the chorion, but does not state if these are in continuity with the vascular elements in the body-stalk.

TRIEPEL (1917).

Abortion. Embryonic shield 1.6 mm. In the embryonic shield projections between the mesoderm and entoderm are taken to represent fine vessels. In these no trace of blood-cells is found. The endothelial



heart-tube is not recognisable. The mesoderm of the yolk-sac possesses blood-cells and vessel anlagen in great numbers. Near the anterior end of the yolk-sac extra large blood-islands are found. He finds that both blood cells and vessels arise from the mesoderm, but considers that in a few places cell processes of endoderm take part in the vessel formation. He concludes, however, that the vessel-forming potentiality of the mesoderm is greater than that of the endoderm. In the middle of the yolk-sac a few quite separate "Erythrocytes" are found. These are nucleated cells. The body-stalk has at its middle short representations of vessels which can be followed only through one or two sections. The villi show the presence of channels regarded as the anlagen of vessels, but these contain no blood-cells. In the mesoderm of the amnion near the body-stalk are a few isolated blood-cells.

#### INGALLS (1920).

Curettage. Embryo, greatest length 1.38 mm. Ovum  $7.5 \times 10.5 \times 12$  mm. In this embryo the pericardial coelom is present, a heart plexus has formed, and the dorsal aortæ and the rudiments of two aortic arches are evident. In the yolk-sac vessels are abundant, especially laterally and posteriorly, but all are not canalised. In the body-stalk are two umbilical arteries and a venous plexus. The chorion contains numerous vessels, many with a wide lumen. Formed elements are present, however, only at the base of the body-stalk. The villi have abundant slender anastomosing channels or cords and many detached strands. One umbilical artery establishes connection with the vascular elements in the yolk-sac wall. The venous plexus of the body-stalk is not in connection with the yolk-sac vessels. "Slender and circuitous" connection between the plexus in the body-stalk and the chorionic vessels is established by small, thick-walled vessels regarded as ingrowths from the chorion to meet the independently formed vessels of the stalk. Vascular structures in the villi are in continuity with the deeper vessels of the chorion. Circulation in the sense of a pulsating heart is not yet established.

#### DISCUSSION.

##### *Yolk-sac.*

Reviewing the specimens considered, we find the following steps in vascular development in the yolk-sac.

The earliest embryo in which vascular development is mentioned is that of SCHLAGENHAUFER and VEROY, who find the *anlagen of blood-islands* present. The first definite statement that *blood-islands* are present is found in MEYER's description of his specimen. Vessels (with endothelium and blood corpuscles) are first encountered in the LEWIS (Minot) embryo. *Vessels having a definite course* over the yolk-sac are found only in ETERNOD's specimen.

Of the embryos earlier in the list than T. B. No. 2, only those of SCHLAGENHAUFER and VEROY and HERZOG show indication of vascular development, and in the latter this is seen not in the yolk-sac proper but at its junction with the body-stalk. Following on T. B. No. 2, blood-islands are present in all the specimens. The thickenings or grouping of cells in the mesoderm of T. B. No. 2, present also in FETZER and v. MOLLENDORFF's Op., are almost certainly blood-islands in the process of formation. With reference to the collection of mesoderm cells in T. B. No. 2, which lies between mesoderm and endoderm, it is interesting to note that v. MOLLENDORFF in his ovum "Op." describes a similar solitary collection which he also regards as of mesodermal origin.

The M'INTYRE specimen appears after several (LEWIS, GROSSER, INGALLS (1918), and FRASSI) in which vessels are clearly formed. From the description given it is obvious that the term "vessel" cannot be correctly applied to the most mature form of blood-island which I have described. This doubtless represents a variation within normal limits. Another

example of this variation is found in STRAHL's specimen, in which vessel anlagen are described merely as thickenings in the mesoderm of the yolk-sac wall.

*Regarding the Distribution of the Blood-Islands.*—In all specimens where definite mention of the distribution of the blood-islands is made, only one (INGALLS (1920)), corresponds at all closely to the arrangement in the M'INTYRE embryo. In the remainder, with two exceptions, the blood-islands are present, or furthest developed on the ventral or distal pole. In the THOMPSON and BRASH case, although the blood-islands are situated on the ventral pole, they are more advanced in development at the cranial extremity. TRIEPEL, in his embryo, finds the largest blood-islands at the anterior extremity. The restriction of the blood-islands to the lateral walls in the M'INTYRE specimen has permitted me to figure them graphically (text-figs. 2 and 3) as they appear in side view of the yolk-sac. I have no explanation to offer for this departure from the arrangement usually described.

*The Source of Cells forming Blood-Islands.*—In the majority of cases the blood-islands are described as being situated in the mesoderm layer, or as producing thickenings or protuberances of that layer (SCHLAGENHAUFER and VEROCAY, STRAHL-BENEKE, LEWIS, STRAHL, and TRIEPEL). In a few cases they are said to lie between mesoderm and endoderm. (MEYER, GRAF SPEE v. H., and GRAF SPEE "Gle."). In MEYER's and in GRAF SPEE's "Gle.," although situated between the two layers, connection to mesoderm is noted. THOMPSON and BRASH, in describing their specimen, hint at the possibility of blood-cell origin from endoderm and endothelium from mesoderm, although they come to no definite conclusion on the matter. TRIEPEL finds in a few places in his ovum that processes from endoderm take part in vessel formation. In the original description of all the human ova considered, with the exceptions mentioned, no statement that blood-islands are connected to or arise from endoderm is encountered.

These facts at first sight might appear to decide the question under consideration, but one has to contend with the possibility of the early migration of endoderm cells into the mesoderm layer, there to give rise to the formation of blood-islands. If we accept the thickenings of the mesoderm present in FETZER, v. MOLLENDORFF (Op.) and T. B. No. 2 as blood-islands in process of formation, then, as proof of endodermal origin, we might expect to find in those cell masses or in parts of them, in addition to mere alteration in arrangement, some slight departure from the appearance of the mesoderm layer in which they lie. If, for instance, we imagine a yolk-cell as the nucleus of one of these cell groups, in well-preserved specimens one would expect to recognise, at least, a different staining reaction of the protoplasm. I have not encountered any statement that such an appearance is present in any specimen in this series, nor is it found in the T. B. No. 2 ovum, which represents a stage at which it would most likely be found if such were the case.

MANN in *Quain's Anatomy* accepts the mesodermic origin of the yolk-sac vessels. In *Keibel and Mall* EVANS also practically accepts a mesodermic origin for the vascular anlagen, but with the reservation that they may actually have arisen from the endoderm. MINOT, in the same work, holds that the angioblast is formed from cells which separate from the yolk, or from the layer of yolk-cells. The most recent work bearing on this problem is that of FLORENCE SABIN, who has been able to observe in the living chick the actual differentiation of mesoderm to angioblast. This work would appear to furnish conclusive proof that in the embryo of the chick, at least, the blood-vessels arise not only in, but from, mesoderm.

WANG believes that in ferret embryos the blood-cells are formed before the endothelium and in connection with the endoderm. Endothelium arises from the mesoderm layer, and growing round and engulfing the blood-cells, takes them into the circulation. The THOMPSON

and BRASH ovum, as has already been noted, is the only one in the human series in which a somewhat similar appearance is described. The vascular elements in the yolk-sac wall of the ferret embryos produce projections on the endoderm side, another appearance not encountered in the human embryo.

The evidence regarding the source of origin of the blood-islands in the human embryo may still be regarded as inconclusive, but the weight of evidence is decidedly in favour of origin from mesoderm.

*The Differentiation to Blood-Vascular Tissue.*—Accepting that the blood-islands in the wall of the yolk-sac take their origin from mesoderm, at what stage does differentiation of mesoderm to blood-island cease? From the descriptions of many of the older specimens, even when vessels are present, it is apparent that early blood-islands also are found. Definite statements regarding the continuity or otherwise of these are not always encountered, but it would appear that the differentiation is progressive, and that these early representations are not the result of growth from the more mature elements. The arrangement in the wall of the yolk-sac in the M'INTYRE ovum at any rate supports this view. The stage at which this differentiation ceases is, I think, a stage beyond that embraced by the material examined or reviewed here.

*Origin of Corpuscles, Plasma and Endothelium.*—Turning now to the separate elements of the yolk-sac vessels, are we to regard the blood corpuscles and endothelium as both arising from the blood-islands? If we regard the blood-island as consisting of the whole thickness of the mesoderm layer where a blood-island exists, then both elements arise from the blood-island. If, on the other hand, we regard only the central part of the total mass (different in appearance to the adjacent mesoderm) as the blood-island, then it is possible that the blood-island is responsible for the production of blood corpuscles, while from the surrounding mesoderm endothelium takes its origin. The former is the view generally held (BREMER, SABIN), but here again in the descriptions of early human embryos there is little evidence one way or the other. JORDAN, in the yolk-sac of a 13-mm. human embryo, finds the latter method of differentiation present. In the M'INTYRE embryo the appearances generally suggest, first, a differentiation into angioblastic tissue which is responsible for production of both blood corpuscles and endothelium.

The most mature form of blood-island in the M'INTYRE ovum represents the stage at which plasma first appears. This arises as a result of splitting-up of the central mass into smaller nucleated masses which no doubt by further division will produce individual cells—the blood corpuscles. STREETER finds “considerable conversion into clear plasma.” SABIN in the living chick finds that whole masses are destroyed in the process of liquefaction to form plasma. A comparison of direct observation of the process with the picture representing an isolated stage is impossible, but it may be said that in the material I have examined there is no evidence of destruction of nuclei in the process of plasma formation. The formation of plasma would appear to occur *pari passu* with the splitting-up of the protoplasmic mass into individual cells. It is not suggested that there is an immediate production of single free cells by this process of cleft formation, but rather that for a time masses of nucleated protoplasm remain attached to the outer boundary of the blood-island (the future endothelium). They are already hæmoglobin coloured and will produce blood corpuscles. They, therefore, represent blood-islands in the sense in which the term is employed by SABIN, and their appearance corresponds to her description of such.

*The Blood-Islands are not continuously connected.*—It will be remembered that in the



M'INTYRE ovum the blood-islands in the yolk-sac are not continuously connected. MEYER states that in his ovum the yolk-sac blood-islands do not communicate with one another. DEBEYRE states that they do not form a network. GROSSER finds the blood-islands already connected together in some parts. In the other ova where blood-islands are present, if not definitely stated, in the majority of cases the description implies that they are not continuously connected. If, as MINOT suggests, the angioblast appears as a reticulate grouping of cells between the mesoderm and endoderm, and maintains its complete independence throughout life, then the yolk-sac blood-islands would be connected up together at all stages and progressive differentiation of mesoderm would not occur. The evidence in human material is entirely against this view. The blood-islands are at first isolated from one another, inter-communication being established later. There is indication that this linking-up of the blood-islands has commenced in the M'INTYRE embryo.

I have not encountered any funnel-shaped arrangement of the mesoderm of the yolk-sac as described by BREMER in JUNG's ovum. The projection of mesoderm cells noted in T. B. No. 2. is solid.

In two cases blood-cells are found free in the cavity of the yolk-sac. STRAHL in his embryo finds nucleated red-blood corpuscles free in the yolk-sac lumen. TRIEPEL describes erythrocytes (nucleated cells) as present in the middle of the yolk-sac. In this connection it is interesting to note that a few cells, in appearance very similar to the nucleated red-blood corpuscles in the stalk, were found in the yolk-sac cavity of the M'INTYRE embryo. They were situated at the angle of junction of the yolk-sac wall and blastoderm on the left side. After careful consideration it was decided that these were endoderm cells heavily laden with yolk which produced a staining reaction of the protoplasm simulating hæmoglobin colouring.

MINOT states that "in man, if red blood-islands occur at all, they must break up very early." That hæmoglobin deposit occurs in the blood-islands of the yolk-sac before these break up is clear from the appearances in the M'INTYRE embryo. This, however, may be a very transitory stage, as MINOT implies.

No endodermal "blisters," as described by SABIN, were encountered in either specimen examined. What were taken to be "blisters" in the mesoderm of the amnion receive mention shortly.

#### *Amnion.*

The earliest ovum in which vessel formation is noted is that of STREETER, where the process is recognised over the greater part of the amniotic mesoderm. ROSSENBECK finds endothelium-lined spaces present. ETERNOD describes early vessel formation, some of the elements of which are canalised. TRIEPEL notes a few groups of blood-cells near the body-stalk. The early vascular tissue present in the M'INTYRE embryo is so near to the body-stalk that I prefer to regard it as part of the vascular development in that area. In this embryo ring-like structures or "blisters" in the mesoderm of the amnion are seen projecting outwards in some of the sections (text-fig. 4), but these were not regarded as concerned in vascular development. I am unable to offer any opinion with regard to their significance.

It is rather remarkable that the STREETER embryo—the earliest in the series in which vascular development is recognised in the amnion—should show comparatively extensive development. More so is this the case when we meet with no mention of the commencement of the process in many older embryos.

*Body-stalk.*

Mention of vascular development is encountered at the earliest stage at which a body-stalk exists, viz. in JUNG's ovum. The cellular collections with lumen described, he does not, however, definitely decide to be vessel anlagen. The next reference is found in HERZOG's specimen, where the anlagen of the yolk-sac vessels are located at the junction of that structure and the body-stalk. The next in order is the earlier of the two specimens under consideration in this paper, and in it two separate regions of the stalk are involved in the process. The angioblastic strands and spaces situated at the base of the stalk indicate essentially the same process as is going on in the chorionic mesoderm. Consideration of this area is deferred until the vessel formation in the chorion is discussed. The question as to whether this process extends upwards into the stalk to represent the ingrowths from the chorion described by INGALLS (1920) will also require consideration. In the body-stalk proper the early commencement of vessel formation in a different manner has been indicated. The drawing reproduced (Pl. I, fig. 4) is not so convincing as the actual specimen. It is reproduced mainly to show, as indicated by the arrow, the possible interpretation that the mass has sunk in from the surface, a point of interest in connection with BREMER's theory of origin of the vessels. The figure, however, demonstrates the difference between the mass and the surrounding mesoderm. There is no doubt that this represents the early formation of blood and vessel, and from its position it probably represents one or other umbilical artery.

In DEBEYRE's embryo the next step in development is found. In the body-stalk blood-islands are described. Two of these are particularly large and elongated, and might well be taken to represent the first recognisable differentiation into umbilical arteries. In ROSSENBECK's specimen we meet with the first open channels. Two endothelium-lined spaces present are described as having a course strikingly like that of the two vessels of the M'INTYRE embryo. The combination of two regular vessel channels with nucleated red cells free in their lumina is first encountered in the latter specimen.

With minor variations vascular development in this region advances steadily in the specimens considered. Two exceptions may be noted, viz. STRAHL's and TRIEPEL's. In the former no blood-vessel anlagen are present, in the latter a somewhat more advanced stage of development than is described might be expected.

Returning now to the M'INTYRE embryo, in the body-stalk we find two umbilical arteries, a venous plexus and isolated angioblastic masses. These last named in some cases resemble the blood-islands of the yolk-sac. Blood-islands in the body-stalk are described by DEBEYRE and INGALLS (1920). From their descriptions it appears that in the former the blood-islands cannot stand in relation to vessel lumina, as lumina are not yet established, while in the latter the blood-islands are situated *in* the vessels. In my specimen the angioblastic tissue is not located in the vessel channels. No blood-islands, in the sense in which the term is employed by SABIN, or as described by INGALLS, are found. Nucleated blood corpuscles are numerous in the umbilical arteries, but no syncytial or cell masses are attached to the vessel walls. My interpretation of this is that the angioblastic masses, as they mature and produce blood-cells, are incorporated in the vessel lumen. This inclusion of these masses of cells must coincide with or follow the freeing of the cells, otherwise their attachment to the vessel wall would have been encountered. In the venous plexus of spaces no free cells are present, but communication partly open and partly solid between the spaces and the angioblastic masses is very

common. Such connection with the umbilical arteries exists, but is not so frequent. Speculating on this, I should offer as an explanation that in the umbilical arteries blood-cells are now being produced partly by multiplication of the existing free blood-cells, whereas, the venous plexus at this stage having none, is entitled to a more generous supply of blood-cell forming tissues.

In describing the walls of the vessels in the body-stalk it was stated that their structure does not entitle one to apply the term "endothelium-lined" to these channels. The inner lining has to undergo further differentiation before it can be so described. It is quite obvious, however, that the lining of these channels will form endothelium. If this is so, then in the plexus of spaces we have tissue which is undergoing differentiation into endothelium in the absence, as yet, of blood-cell contents. Here it may be noted that STOCKARD finds in teleost embryos that the "endothelium is in all cases utterly incapable of giving rise to any type of blood-cell." When spaces become lined by endothelium, blood-cell reproduction stops. "The red-blood corpuscles are always produced so as to be delivered into the vessels. . . ." This description might quite well be applied to the body-stalk of the M'INTYRE embryo. SABIN, however, maintains that it is proved for the chick that endothelium can form erythroblasts.

Finally, with regard to the body-stalk in the M'INTYRE embryo, the condensation of protoplasm and nuclei which forms the walls of the umbilical arteries is a relatively thick layer. This layer is of a greater thickness, one might suppose, than is necessary for the production of a simple endothelial lining. Is it possible that we have here, already, evidence of the commencement of formation of the extra-endothelial structures of the walls? I think one is almost justified in concluding that such is the case.

The commencement of vascular development can be recognised in the body-stalk and yolk-sac at about the same stage. It is usually stated that vascular development can first be recognised in the yolk-sac, but in the human embryo the evidence points rather to a simultaneous commencement of the process in these two regions.

#### *Chorion.*

Among the ova earlier than the T. B. No. 2, in one only (v. MOLLENDORFF'S Op.) is there mention of vascular development in the chorion. v. MOLLENDORFF describes channels which are accepted as vessels, and these are lined with flattened cells. In the T. B. No. 2 ovum we meet with the angioblastic strands and spaces which have been described. Vessels are present in the chorion of DEBEYRE'S and INGALLS' (1918) specimens, and numerous large vessels with plentiful free nucleated red cells have appeared in the M'INTYRE ovum. Recent work on angiogenesis has been directed principally to solving the problem of development of intra-embryonic vessels. In the literature, therefore, one finds the descriptions of vessel development in the chorion less satisfactory than for the regions already considered. A noticeable feature is that a gradual sequence in development is not so readily made out.

The appearances in the T. B. No. 2. ovum are of particular interest and are reproduced somewhat closely in only one specimen, viz. LEWIS (Minot). In the v. MOLLENDORFF (Op.), STRAHL-BENEKE, GRAF v. SPEE (v. H.), GROSSER, and INGALLS (1918) ova, spaces only are found in the chorionic mesoderm. In the LEWIS (Minot) embryo, however, spaces with contained strands, the latter being regarded as collapsed endothelium, are described. BREMER] describes spaces and strands in several ova he examined, but these are found



more particularly in the body-stalk. The v. MOLLENDORFF (Op.), STRAHL-BENEKE, GRAF v. SPEE, and LEWIS specimens all represent a stage in development very near to that of T. B. No. 2, while GROSSER's and INGALLS' ova are slightly older. It would seem almost as if the appearances in the T. B. No. 2 ovum, which have been detailed in the early part of this paper, were present only for a very short period. There is nothing comparable to these spaces found in the M'INTYRE ovum or, as far as one may judge from the descriptions, in other specimens representing a similar or a later stage in development.

In the descriptive part of this paper I have suggested a reason for the presence of the spaces in the chorionic mesoderm, and have recognised that they may have become exaggerated by adventitious influence. I have also advanced some proof that the strands which they contain represent early phases of vessel-formation, that, in short, they are angioblastic strands.

In T. B. No. 2, although an occasional space communicates with the cavity of the vesicle, no connection of angioblastic strands with the inner surface of the mesoderm layer was encountered. The strands and spaces, already mentioned, at the base of the body-stalk differ in no respect but size from those elsewhere in the chorion. The area where they lie it is impossible to allocate with any certainty to either body-stalk or chorion, but as the appearances are essentially the same as in the chorion, I prefer to regard it for descriptive purposes as chorionic. Away from the chorion there is no indication of downgrowth in the body-stalk of angioblastic tissue into the chorionic mesoderm. The possibility of migration of endoderm cells from the yolk-sac to the chorionic mesoderm, there to provide the origin for angioblastic formations, has never been suggested. We must conclude, therefore, that in the chorionic membrane angioblastic tissue arises by differentiation of the mesodermic elements.

With reference to the M'INTYRE embryo, blood-islands as described in the yolk-sac are not encountered in the chorion. In the chorion the vessel and blood-forming tissue is present in more elongated form. Although wide vascular channels containing nucleated red cells are found, these can always be traced a considerable distance in the wall of the chorion. The earlier types in their narrow elongated form give the impression that there is considerable effort to produce rapidly channels with a lining destined to form endothelium. In the yolk-sac, on the other hand, the effort would appear to be directed more to the forming of blood-cells. Even in the chorion, nevertheless, as soon as a channel exists, the presence of primitive blood-cells can be made out.

The collected evidence points to the commencement of vascularisation of the chorion as occurring at about the same time as it commences in the yolk-sac and body-stalk. This would correspond to a stage in development represented by an ovum slightly younger than the T. B. No. 2. In practically all the specimens older than T. B. No. 2 vascularisation of the chorion is noted in some form or other.

#### *Villi.*

Descriptions of the process of vascularisation of the villi are even less satisfactory than those of the chorion. In the list of specimens surveyed, the process receives notice first in STREETER's ovum, in which solid strands and endothelial tubes are present. DEBEYRE refers to doubtful early vessel formation. In INGALLS' (1918) ovum, and in the majority of those older than his, vessels can be recognised. It is apparent that vascularisation of the villi commences at a later stage in development than is the case in the yolk-sac, body-stalk, and chorion.

In the M'INTYRE embryo there is no difference in the process of vascularisation as seen in the chorionic membrane and in the villi except in degree. In the T. B. No. 2 there is no proof that the (empty) spaces present in the mesoderm of the villi are concerned in vascular development. It is possible that these spaces might later take on the characters of those in the chorionic mesoderm and contain similar angioblastic strands. If such a stage exists for the villi, it has not been described. The presence of angioblastic tissue isolated in villi, as seen in the M'INTYRE embryo and as described by INGALLS (1920), entitles one to assume that here again such masses result from differentiation of the mesodermic elements *in situ*.

#### *Pericardium and Heart.*

Of the ova earlier than ETERNOD'S, in three only does mention of the presence of vascular development in the embryo appear. v. MOLLENDORFF (Op.) finds one group of cells of doubtful significance; DEBEYRE thinks a cellular collection present may represent the first cardiac formation; ROSSENBECK suggests the possible presence of the anlage of the aorta.

The failure to find, after a careful search, any appearances in the M'INTYRE embryo indicative of the commencement of the aortic or heart rudiments makes it more than probable that the findings in these three specimens cannot be interpreted as suggested by those who have described them. The description of the FRASSI embryo, also definitely more advanced in development than the three mentioned specimens, would bear out this contention. The sudden transition to the presence of a heart and an established circulation in ETERNOD'S ovum seems almost too sudden to be accepted as normal. In GRAF SPEE'S "Gle." EVANS finds the cardiac endothelium commencing, and INGALLS' (1920) embryo has a heart plexus, dorsal aortæ and aortic arches. From the latter at least it is a very short step to an established circulation. The size of the ovum or of the embryo we now also know cannot be taken by itself as an indication of the stage of development. It must be conceded, however, that, as described, the cardio-vascular development of ETERNOD'S ovum has probably been a little precocious. For comparison, it is interesting here to note that SABIN finds in the chick that in the embryo the angioblast can be seen to differentiate from mesoderm at the stage of five somites, and that the heart-beat may be established at the stage of ten somites.

With regard to the formation of the pericardium, INGALLS in his 1918 ovum regards tubular ingrowths (two on either side) from the extra-embryonic coelom as standing in some relation to the future pericardial cavity. If this is the method of origin there is certainly no trace of any communication between the "U"-shaped cavity in the M'INTYRE embryo (which conforms to the description given by ROBINSON for mammals in 1903) and the extra-embryonic coelom. The material and the literature I have examined throws no further light on the earliest phase of pericardial formation in the human.

#### *Yolk-sac Prolongations and Mesoderm Strands in the Chorionic Vesicle.*

The yolk-sac connection to the chorion in the T. B. No. 2 ovum is so well established and so accurately described by BRYCE that particular attention is directed to this type of structure in relation to vascular development. In FETZER'S ovum a process from the yolk-sac ends free in the chorionic vesicle, and has no particular relation to vessel formation in the yolk-sac. It is rather curious that the following three ova showing yolk-sac

prolongations extending to the chorion should appear in direct sequence in the list. These are the T. B. No. 2, MEYER's and STRAHL-BENEKE's. In two of these, viz. T. B. No. 2 and MEYER's, the strand from the yolk-sac terminates in relation to a space or spaces in the chorionic mesoderm which are in some way related to vascular development. In the former, angioblastic strands are more plentiful there than at any other part of the chorion, with the exception of the base of the body-stalk, while in the latter a blood-island is present, although these are absent elsewhere from the chorion. The similarity in appearance in some respects at this area, in these two specimens, has already been indicated. In the T. B. No. 2 ovum the yolk-sac prolongation, after reaching and running on the inner surface of the chorionic mesoderm for a short distance, is replaced by an elongated protoplasmic mass of mesoderm which ends free in the chorionic cavity. This projection is traversed by a space which contains angioblastic strands. In the wall of this space the yolk-sac prolongation finally terminates. The strands in the space attract particular attention. BRYCE, in his memoir, reproduces a section through this area (Pl. iv, fig. 18), showing a lumen in the angioblastic strand present. I have made drawings of the strand or strands in the individual sections, and after very careful consideration I have come to the conclusion that the lumen present cannot be definitely accepted as an early vessel channel. As this question is one of some importance, it will be necessary to give a brief description of the appearances in this region.

From the first section, after the endoderm elements have disappeared from the wall of the space, the space can be traced through forty-nine sections. In the first section, after the yolk-sac duct terminates, the space has just been formed by the running together of several spaces. From here onwards it does not branch. Throughout the sections the space, as far as one can judge, has been cut more or less at right angles to its long axis, except in the last three or four sections where it has been cut obliquely. In the first section there appear three strands, two of which both show one nucleus present and the third five nuclei. The next shows four strands having respectively one, three, five, and six nuclei, and these strands lie in the space equidistant from one another, so that if their margins came in contact a lumen would be established. The third section shows only one strand which as cut across has the form of the letter "C," while, in the fourth, in which fourteen nuclei can be counted in the strand, the gap in the "C" is almost but not quite closed. In the next two the "C" shape is maintained, but has opened up considerably. In the succeeding seven sections the strand appears in one, two, or three portions. There is no suggestion of a lumen, but where the strand is in one portion only it has a double curve in the form of the letter "S," one extremity showing attachment to the wall of the space. The next section, the fourteenth from the one first considered, shows the strand "U"-shaped in section. In the succeeding section it is "L"-shaped, and the next section in order is that figured by BRYCE where a closed circle is undoubtedly present. In the next section (seventeenth) the strand appears in three parts where again, if one imagined the adjacent margins in apposition, a lumen would be present. The subsequent section shows four strands; the nineteenth, one strand (attached to wall of space); the twentieth, five strands (two attached to wall of space); the twenty-first, four strands, while in the twenty-second there is but one strand "C"-shaped in section. From here onwards in the twenty-seven subsequent sections the strands vary in size and number, but never again suggest the possibility of a lumen—complete or incomplete.

The possibility that the break in the "C"-shaped form, of which there are five examples, is accidental, and that there was in reality a lumen present, must be taken into account. Even if the break in the circle in these sections has been produced in the course of



preparing the material, I still think these forms, including the particular one described by BRYCE, do not represent channels or tubular cavities in a strand. My interpretation is that the angioblastic strand in this particular space is constantly dividing into branches, and being joined by new branches which run parallel to one another, and that the lumen represents a space around which several branches have joined up to form one. The space, therefore, I regard as not situated in a strand but as part of the space in which the strand lies. From the M'INTYRE ovum it is clear that the earliest vessel channels arise as closed spaces within the angioblastic strands. I have come to the conclusion, therefore, that in the T. B. No. 2 ovum there is no canalisation of the angioblastic strands in the chorion, but that these are still solid.

In the STRAHL-BENEKE ovum the yolk-sac prolongation to the chorion possesses no early vascular elements, and although spaces are described in the chorionic mesoderm these do not appear to be specially prominent at the attachment of the structure. ROSSENBECK describes two mesodermic strands running from the amnion to the chorion (one through the body-stalk), and these end in connection with vessel anlagen in the chorion. GROSSER's ovum possesses a prolongation of the yolk-sac to the chorion, and in the wall of one of the entodermal cysts which this structure contains blood-islands are present.

These connections between the embryonic mass and the chorionic mesoderm must have some relation to vascular development, but the information at present available does not furnish an explanation of this relationship. BRYCE mentions GROSSER's suggestion that this "might be a reminiscence of a stage in the phylogeny of the primates in which there was a yolk-sac placenta." I am prepared to state that, after careful examination of one specimen in which such a communication is present, I can find no evidence to indicate that the yolk-sac endoderm has any relationship to the angioblastic tissue present. This is contrary to MEYER's findings.

#### *Continuity of Vascular Tissues.*

The question of the continuity of the vascular elements has already been discussed with regard to the yolk-sac, and may now be considered for the other regions of the ovum, first individually and later collectively. In the body-stalk, while still at the stage of angioblastic masses or blood-islands, the umbilical arteries are being defined. This stage is represented by DEBEYRE's ovum where two elongated blood-islands might be regarded in this light. Plexus formation in the case of these arteries must represent a very transitory phase, as in ROSSENBECK's ovum while still referred to as "anlagen" they have a course corresponding closely to that of the umbilical arteries in the M'INTYRE ovum. In the case of the veins, the plexiform phase would appear to be of much longer duration, as it is still present in INGALLS' (1920) specimen and to a lesser extent in ETERNOD's.

As regards the chorion, definite statements are rarely encountered. ROSSENBECK, however, finds the chorionic vessel anlagen not continuously connected. This is in agreement with the appearances in the T. B. No. 2 ovum, and also in the M'INTYRE ovum. At this stage it is interesting to note that in a number of these early ova the area in the vicinity of the body-stalk shows a more advanced vascular development than elsewhere in the chorion. This is found both in the T. B. No. 2 and in the M'INTYRE specimens. INGALLS (1918) finds vessels by far most frequent near the attachment of the body-stalk. FRASSI recognises vessel anlagen with certainty only near the body-stalk. In the INGALLS' (1920) specimen, where vessels are abundant, formed elements are found only at the base of the body-stalk. As it is already clear that in the human ovum the information we have is entirely against a progressive

growth of vascular tissue outwards from the body-stalk, this can be regarded only as an early indication of differentiation of placenta from chorion. It is probable that at no stage of development is the chorion equally well vascularised throughout. Similarly, the villi at different points of attachment to the chorion, from the beginning, are vascularised in varying degree. Two ova indicate an independent origin for the vessels in the villi. These are the M'INTYRE and INGALLS' (1920) specimens. From human material, therefore, the evidence collected would indicate that in the different areas the vessels have their origin not in one angioblast but by progressive differentiation at many points into angioblastic tissue.

Turning now to a consideration of the continuity of the vascular tissues in the different regions, we again find in many of the specimens considered absence of definite statements on this question. Where vascular elements are recognisable in both the yolk-sac and the body-stalk one is frequently disappointed to find absence of a definite statement that these are, or are not, connected up with one another.

In the T. B. No. 2 ovum, if the interpretation of the appearances is correct, then one may assume that there is no extension of vascular tissue from the yolk-sac to the body-stalk. Similarly one may conclude that there is at this stage no extension of angioblastic tissue from the body-stalk to the chorion. This ovum, however, suggests the possibility of extension of angioblastic strands from the chorion into the body-stalk to communicate with vessels formed independently in the latter structure. This has already been suggested by INGALLS from observations on his 1920 specimen, and the appearances in the T. B. No. 2 ovum lend some support to his view. Possibly it is not so much an extension of vascular tissue into the body-stalk as a taking up of the chorionic mesoderm and its contained vascular elements to assist in the formation of this extremity of the stalk.

Here one might again refer to the distribution of the angioblastic strands and spaces in the T. B. No. 2 ovum. These are well distributed throughout the chorionic mesoderm, and although smaller and less numerous in the vicinity of the vegetative pole, are nevertheless present in that area. In the M'INTYRE specimen no vessel or vessel-forming tissue is found in the chorion except around the attachment of the body-stalk. What has become of the angioblastic strands near the vegetative pole of the T. B. No. 2 ovum? These strands must either have reverted to mesodermic tissue, or the mesoderm in which they were situated has, in the course of enlargement of the chorionic vesicle to the size it has attained in the M'INTYRE ovum, gradually moved round to the vicinity of the body-stalk.

Continuity of vascular tissue in the body-stalk and chorion is established in ROSSENBECK'S ovum. Vascular communication between the yolk-sac and body-stalk is found in INGALLS' (1920) ovum where open communication with the right umbilical artery exists. The M'INTYRE ovum is especially interesting in this respect, that it presents a stage at which the umbilical arteries are well formed but do not communicate with the blood-islands of the yolk-sac; nor does it appear that they communicate with the venous plexus in the body-stalk.

In INGALLS' (1920) and the M'INTYRE specimens continuity of angioblastic strands or vessels in the chorion and in the villi in some cases is established.

From consideration of human material we may conclude that the vessels arise independently in the different regions of the embryo, and that at an early stage the body-stalk vessels are linked up with those of the chorion before vascular communication is established between the yolk-sac and the body-stalk. The only apparent exception to this might be found in the body-stalk as already explained. There is absolutely no evidence that the vessels in the body-stalk result from extension of the yolk-sac vessels as has been suggested.

The question of establishment of vascular communication with the embryo proper does

not come within the scope of this paper, but it is clear from the descriptions of the various specimens that the vascular tissues in the areas here considered are connected up before communication with the embryonic area is established.

Much has been written about the origin of the intra-embryonic vessels because a proof of their independent origin in the embryo settles the question of the possibility of origin of vessels *in loco*. A very complete review of the literature and experimental work in this connection is given by M'CLURE in his presidential address to the American Association of Anatomists, 1921. He concludes that the angioblast theory of HIS, in which it is maintained that the vascular tissue in the embryo is an ingrowth from the yolk-sac, no longer holds, and "that the general principle of a local origin of intra-embryonic endothelium has been completely confirmed by experiment." Some additional evidence from human material that the "general principle" holds also for the extra-embryonic vascular development is supplied in this paper.

Returning now to the *work of Bremer*, the appearances in the T. B. No. 2 ovum in some respects conform to the descriptions and theories he offers. Spaces and strands are present abundantly in the chorion and at the base of the body-stalk, but do not fulfil BREMER's description in that neither forms a continuous network, and therefore, cannot have arisen by direct extension from the body-stalk. No connection of spaces or of strands with the mesothelium of the body-stalk could be made out. Spaces in the chorionic mesoderm may communicate with the extra-embryonic coelom, but no mesothelium is present. The angioblastic mass shown in Pl. I, fig. 4, lying at a higher level in the body-stalk might be regarded in the one section reproduced as having arisen by a sinking in of the surface. Even if this mass were in continuity with the surface, it is unconnected with the spaces and strands at the base of the stalk. These spaces with their contained strands I have already suggested belong to the chorion rather than to the body-stalk, and a theory regarding their method of formation and their significance has been propounded. In the case of the M'INTYRE embryo, the conditions present are against BREMER's contention that "no surely isolated endothelial cords have been found in the chorion." In the body-stalk of this specimen, however, the appearances are certainly in some cases very suggestive of a communication between the surface and the developing vessels through the medium of solid strands. One of these is reproduced in Plate III, fig. 11. We may, therefore, conclude that the mesothelium of the body-stalk may play some rôle in vascular development in that part of the ovum, but that extension of this vascular tissue into the chorion and villi does not occur. The latter postulation is dependent on assuming that the spaces and strands in the chorionic mesoderm of T. B. No. 2 are the same as those described by BREMER. The appearances correspond sufficiently closely to warrant this.

In reading through the *literature* some difficulty is experienced on account of the wide range of terms employed to denote vascular elements and their different forms. For instance, in reference to the yolk-sac, does "the first anlagen of blood-vessels" represent a less mature or a more mature stage than "blood-islands"? I have been content to employ some of the existing terms, but I think a simplification of the terminology merits the consideration of embryologists. Throughout, I have restricted the term "vessel" to those instances where there is a lumen containing free blood-cells. In some of the specimens it is quite obvious that the vascular development has only received passing mention, and no doubt, if all the specimens here considered were examined by one and



the same individual, the record would show many differences. In some cases, notably STREETER'S, DEBEYRE'S and INGALLS' (1920), the vascular development receives special notice. The personal factor may to some extent come into play in recording the picture of the vascular system in isolated specimens. The identification of the very earliest representation of angioblastic tissue can be submitted only as an expression of opinion. The method of recording in this case adopted by one whose work did not previously necessitate a knowledge of the literature was as follows. In the first instance a complete examination of the material was carried out, the findings recorded, and illustrations prepared. This explains the small number of references to the literature in the descriptive part of the paper. An investigation into the literature was then made, and subsequently the material was again examined and a few additional drawings prepared. Some alterations in the original description were necessary, but where doubt arose the first interpretation was allowed to stand. The very favourable plane of section in the case of the M'INTYRE specimen was of the greatest help in investigating the continuity of vascular tissues.

The work in connection with this paper was carried out partly in the Anatomy Department of the University of Glasgow, and partly in the Pathological Department of the Royal Samaritan Hospital for Women, Glasgow. I am responsible for the drawings reproduced, with three exceptions, viz. Plate I, fig. 3, by Mr A. K. MAXWELL; text-fig. 8, which is reproduced from Professor BRYCE's paper; and text-fig. 4, a photomicrograph which Professor TEACHER was good enough to prepare for me. For these illustrations and for many helpful suggestions from Professors BRYCE and TEACHER I wish to tender my sincere thanks. I wish also to acknowledge the privilege of being allowed to examine the sections of the ova, Teacher-Bryce Nos. 1 and 2.

The Carnegie Trust for the Universities of Scotland has made a grant to the Author to defray the expenses of reproduction of the illustrations. This grant is very gratefully acknowledged.

#### CONCLUSIONS.

From a consideration of the material here recorded, and from a review of the literature, the following conclusions are set forth. Some of these may not appear to be fully justified by the evidence supplied, and are, therefore, to be regarded to some extent as opinions rather than conclusions.

1. The blood-vascular system in the earliest stages of development in human ova arises in the extra-embryonic areas by progressive differentiation of mesoderm at multiple points *in situ*. Its commencement may be recognised while yet absent in the embryonic area proper.

2. The theory of vascularisation of the chorion and villi by centrifugal growth of angioblastic tissue from the yolk-sac or body-stalk does not hold for the human ovum.

3. Differentiation to angioblastic tissue occurs at about the same time in the yolk-sac, body-stalk and chorion, while it appears at a slightly later stage in the villi. The first differentiation to angioblastic tissue occurs at a stage just earlier in development than that represented by the T. B. No. 2 ovum.

4. The vascular elements in the separate areas become connected together and the different areas establish connection with one another in the following order: 1. Body-stalk, and chorion. 2. Chorion and villi. 3. Body-stalk and yolk-sac. 4. Yolk-sac, body-stalk and embryo.

5. From examination of the M'INTYRE embryo the impression was formed that in

the wall of the yolk-sac the main effort is directed to the rapid production of blood-cells, whereas in the body-stalk, chorion, and villi channel formation is of equal importance to blood-cell production.

6. Prolongations of the yolk-sac across the blastocyst cavity to the chorionic wall have some bearing, not properly understood, on vascular development in the chorionic membrane. It does not appear, however, that the endoderm elements which these may contain have any part in the origin of the vessels in the chorion.

7. Vessel formation in the body-stalk outpaces that in the other regions, so that the first channels which can be identified as vessels having a recognisable course are those destined to be the umbilical arteries.

8. The arterial and venous systems in the body-stalk do not communicate with one another or, if they are ever in communication in that structure, they become isolated from one another at a very early stage.

9. Blood-cell forming tissues in the body-stalk communicate with the vessel channels but do not *project* into these channels.

10. The mesothelium of the body-stalk *may* play some part in vessel formation.

11. Extension of vessel growth does not take place from the body-stalk into the chorion, but there is some evidence that the reverse process may occur in connection with the venous channels in the body-stalk.

12. In the earliest stage at which angioblastic tissue is found in the chorionic mesoderm, it appears in the form of nucleated protoplasmic strands which run in spaces. These strands are destined to form vessels and blood-cells, while the spaces are regarded as a temporary provision for the ready diffusion of substances for the nutrition of the ovum and, more particularly, of the angioblastic tissues which the spaces contain.

13. At the stage at which angioblastic tissue appears in the chorionic mesoderm, the latter possesses no mesothelium, and, therefore, mesothelium in this region has no rôle in vessel formation.

14. At a very early stage of development the distribution of the vascular tissues in the chorion indicates a differentiation of the area around the body-stalk towards placenta.

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DESCRIPTION OF PLATES.

(A scale indicating the magnification is supplied with each drawing taken from the sections.)

PLATE I.

Fig. 1. Teacher-Bryce ovum No. 2. Wall of chorionic vesicle showing an inner mesothelium-like layer (Mth.), a reticulate zone (Rz.), mesoderm (Mes.), and the trophoblast (Tr.).

Fig. 2. Teacher-Bryce ovum No. 2. Wall of chorionic vesicle including the base of a villus. The mesoderm contains spaces, in one of which a large angioblastic strand appears in cross section (A). C., cavity of chorionic vesicle; V., villus; Tr., trophoblast.

Fig. 3. Teacher-Bryce ovum No. 2. Drawing by Mr A. K. MAXWELL of a medium-sized angioblastic strand and space in the chorion.

Fig. 4. Teacher-Bryce ovum No. 2. Drawing from a section through the body-stalk to show a space containing early blood-cells (Bc.), situated near the embryonic extremity of the stalk. The mesothelial covering on the surface (M.) is apparent, and its possible relationship to the space is indicated by the arrow. S., surface of body-stalk.

PLATE II.

Fig. 5. Teacher-Bryce ovum No. 2. Yolk-sac wall showing a small mass (blood-island?) between endoderm and mesoderm. M., mesoderm; E., endoderm.

Fig. 6. The same mass as in fig. 5 two sections removed, showing protoplasmic connection with the mesoderm layer. M., mesoderm; E., endoderm.

Figs. 7-10. M'INTYRE embryo. Examples of the four stages of blood-island formation in the wall of the yolk-sac as described in the text. M., mesoderm; E., endoderm.

PLATE III.

Fig. 11. M'INTYRE embryo. The field embraces the dorsal part of the body-stalk on one side. The amnion wall (Aw.), is seen passing off from the stalk. Near the angle between the amnion wall and the body-stalk a depression of the mesothelium (Mth.) runs towards an angioblastic mass (Am.), which at this particular level may almost be regarded as a vessel. A., cavity of amnion.

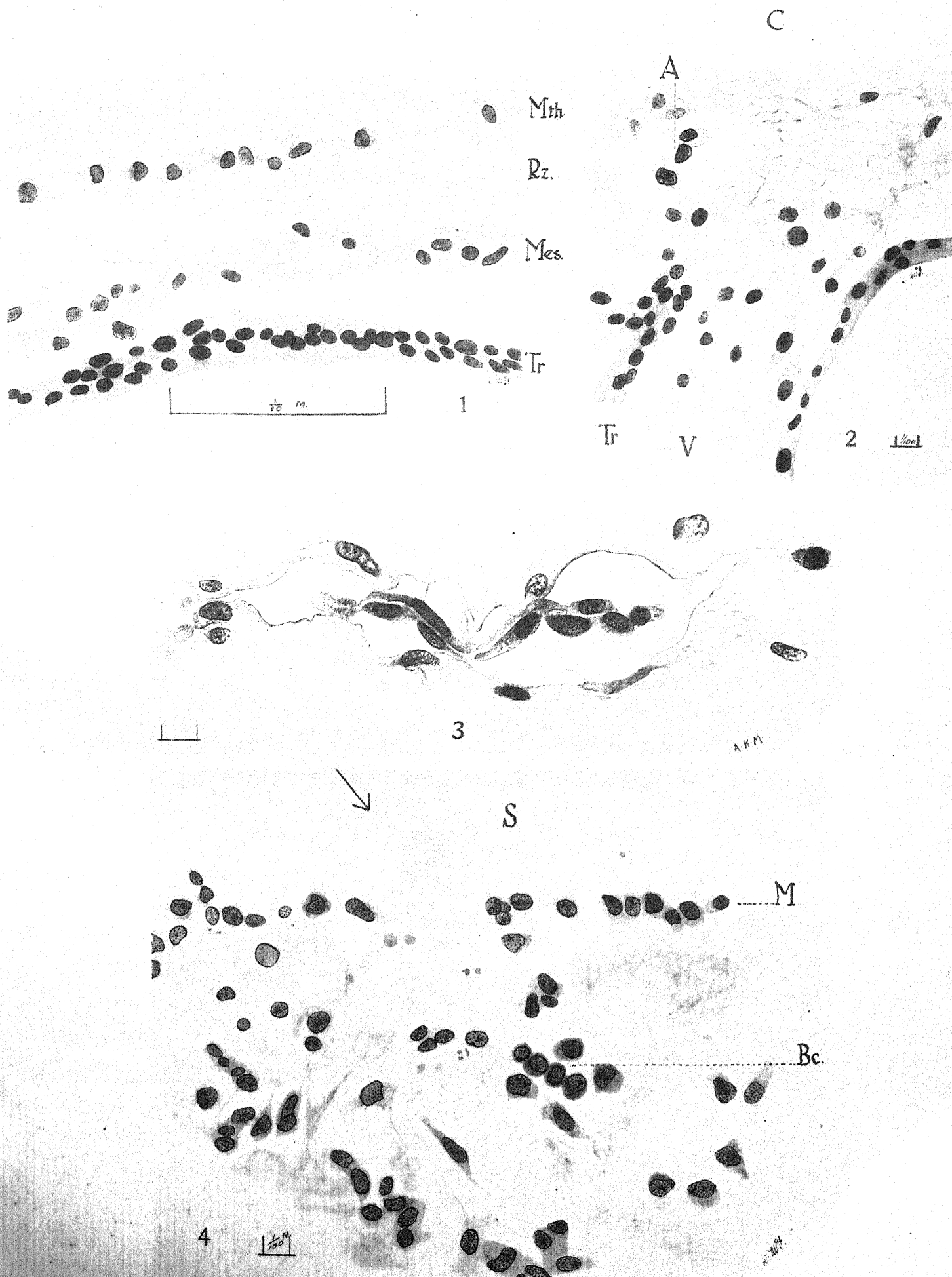
Fig. 12. M'INTYRE embryo. Wall of chorionic vesicle showing condensation of protoplasm and nuclei to form the earliest representation of an angioblastic strand (As.). Tr., trophoblast; M., mesoderm of chorion.

Fig. 13. M'INTYRE embryo. Chorionic mesoderm showing the presence of an angioblastic strand in which haemoglobin-coloured cells have appeared.

Fig. 14. M'INTYRE embryo. A further stage in development of the chorionic vessel is shown. Contained blood-cells are seen and a lumen is present for some distance.



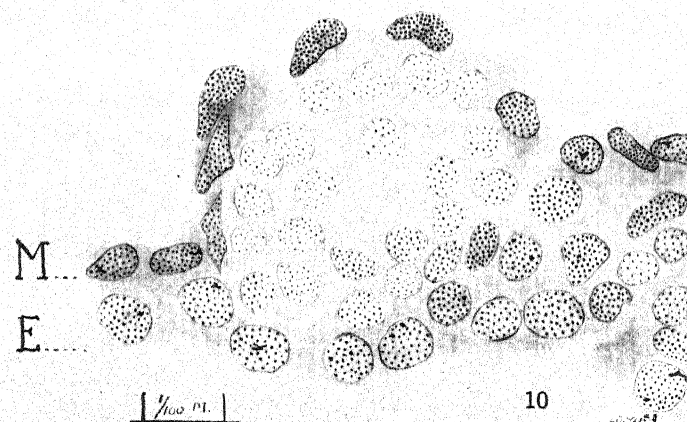
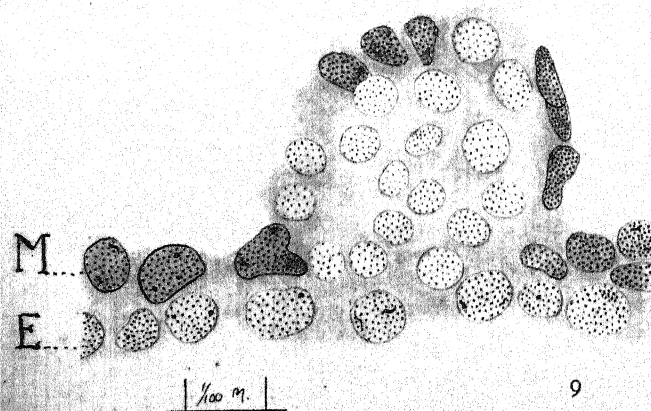
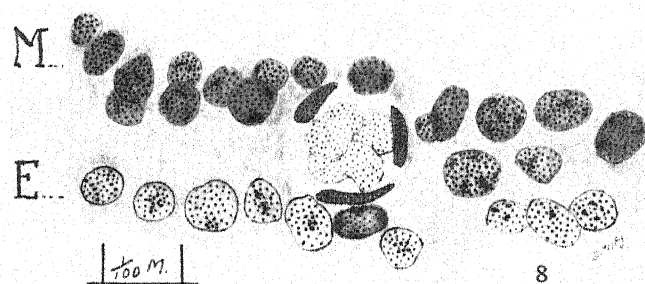
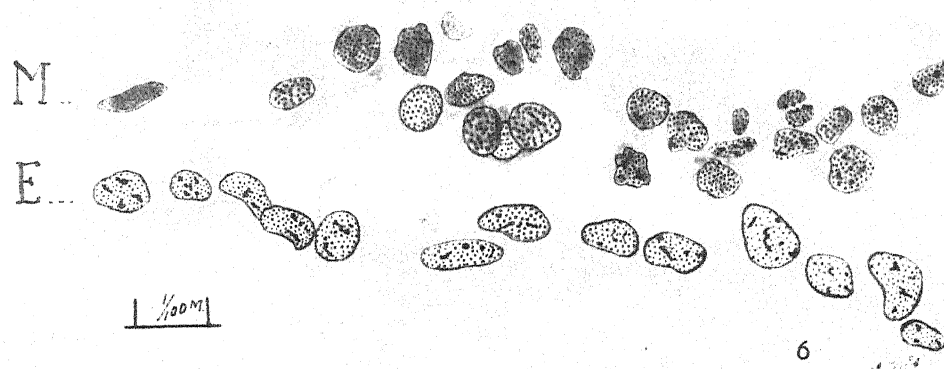
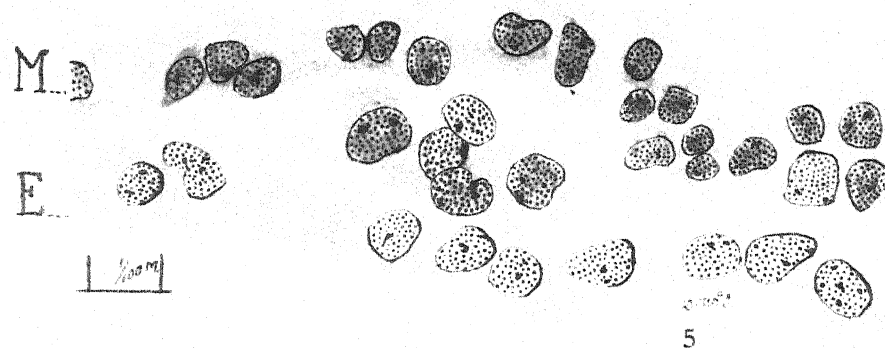
DR. D. MCINTYRE—VASCULAR SYSTEM IN THE HUMAN EMBRYO,  
PRIOR TO THE ESTABLISHMENT OF THE HEART.







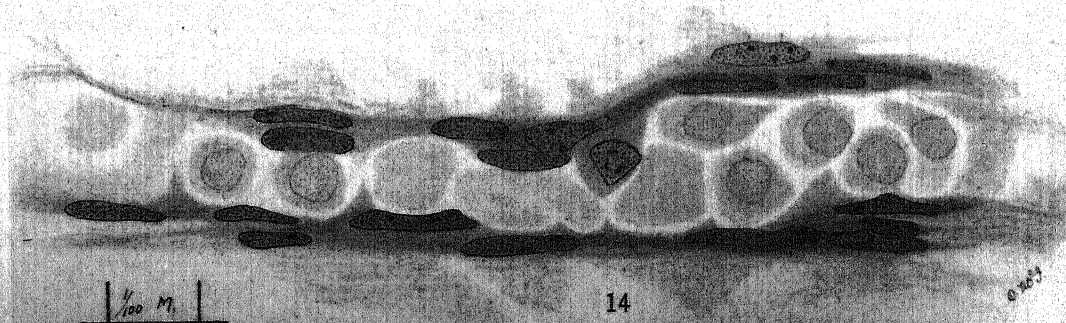
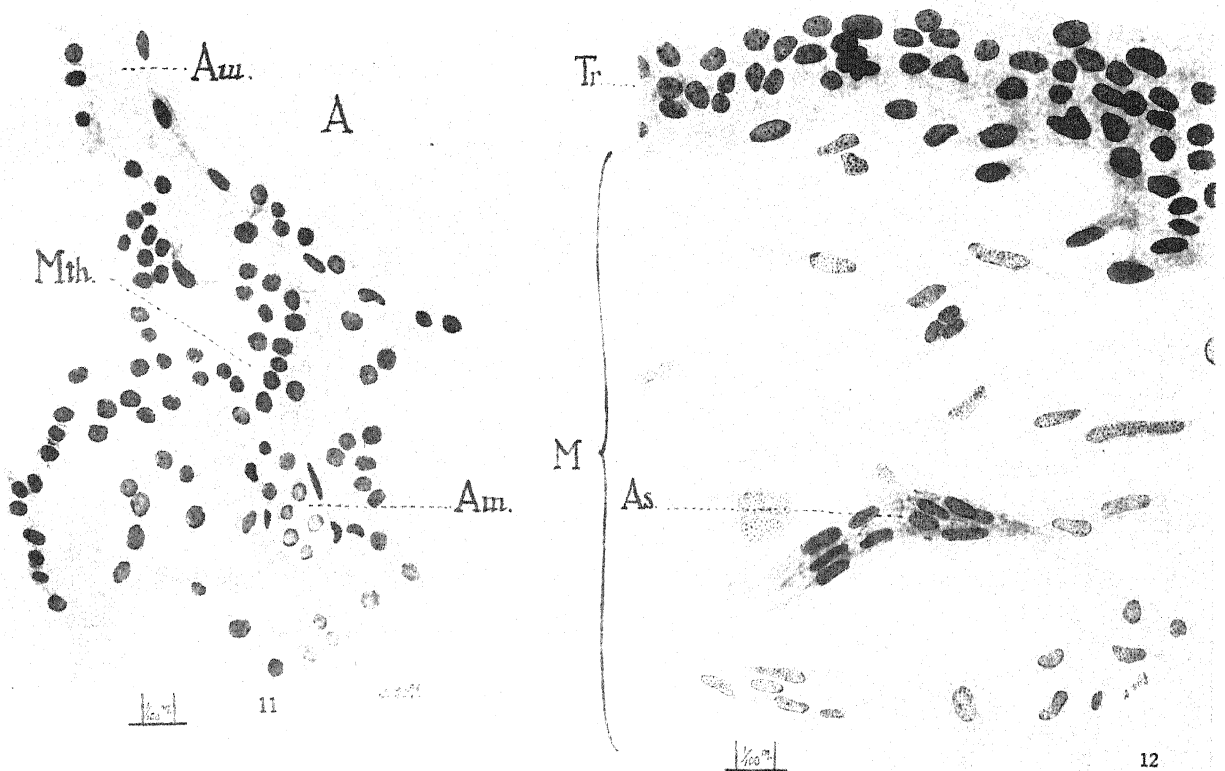
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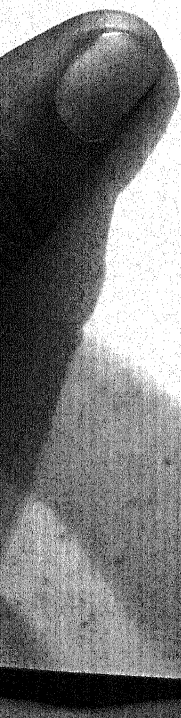






DR. D. MCINTYRE—VASCULAR SYSTEM IN THE HUMAN EMBRYO,  
PRIOR TO THE ESTABLISHMENT OF THE HEART.





V.—Development of *Cavia*: Implantation. By Norman MacLaren, Ph.D., F.L.S., Lecturer in Embryology, Anatomy Department, University of Glasgow. Communicated by Professor THOMAS H. BRYCE, F.R.S. (With Three Plates and Five Text-figures.)

(MS. received June 19, 1926. Read July 5, 1926. Issued separately November 18, 1926.)

INTRODUCTION.

Since GRAF V. SPEE'S admirable work *Die Implantation des Meerschweincheneies in die Uteruswand*, published in 1901,\* little has been done to add to our knowledge of the implantation of the embryo of *Cavia*. His deductions seemed conclusive and passed almost unchallenged into the general literature as an essential part of our knowledge of mammalian embryology.

GRAF V. SPEE'S general conclusion was summed up as follows: "Die daran gemachten Befunde aber führen zu der Erkenntniss, dass das seit seiner Befruchtung noch nicht gewachsene Ei des Meerschweinchens wie ein schädlicher Parasit zunächst das Uterusepithel, dann das subepitheliale Uterusbindegewebe angreift und vernichtet, um sich in der Uteruswand einen Platz zu verschaffen, in den es sich einpflanzt und nachher erst in eine Art Symbiose mit dem Uterus eintritt, die ihren Ausdruck in der Placentarbildung findet."

The essence of this interpretation is that the implantation cavity is produced outside the uterine lumen by a destruction of the subepithelial connective tissue after the embryo has become attached to the epithelium, and has, as it were, eaten its way through it. It has become implanted by the destructive activity of its own cells in the connective tissue of the uterine mucous membrane, whereas in the mouse, rat, and vole the implantation cavity is primarily part of the uterine lumen from which the epithelium has disappeared. As a matter of fact, apart from the more extensive destruction of the uterine tissue in *Cavia*, the end result is much the same in both cases. The object of the present paper is to demonstrate an alternative interpretation of the primary phases of implantation in *Cavia*, which brings them more into harmony with what occurs in *Mus* and other forms in which an actual penetration of the epithelium does not occur.

EMRYS-ROBERTS † and HERMANN and STOLPER, ‡ more recent writers on the problem presented by *Cavia*, have contributed figures and descriptions of some of the phases of implantation, but have accepted the root idea laid down in GRAF V. SPEE'S paper.

A complete series of embryos has been obtained from the much later stage in which the splanchnopleuric folds have met and the gut is closed, down to the stage represented by fig. 1, Plate I § (24 A, a free blastocyst with the zona radiata intact). Obviously, the implantation process is not concerned with embryos at younger stages than 24 A. But though the stages of development anterior to this phase are still unknown, yet we are now in a position to homologise the component parts of a blastocyst of this age with those of other mammals at similar phases of development.

\* *Zeitschrift f. Morphol. u. Anthropol.*, Bd. iii, p. 132.

† *Journ. of Anat.*, vol. xlv.

‡ "Zur Syncytiogenese beim Meerschweinchen," *Sitzungsber. d. K. Akad. d. Wiss. Wien. Math. Naturwiss. Klasse*, cxiv Bd., x Heft, Abt. iii, 1905.

§ These figures are merely the catalogue numbers of the embryos in my collection.



The technical difficulties met with are considerable. The tube and uterus must be cut from end to end and, the egg is so small that one dare not lose a section. A complete series of several thousand sections is thus necessitated for each uterus; and the individual may be sterile. Again, in course of this work it was discovered \* that placental remains simulating ova, morulae and even blastocysts are of common occurrence, either free or embedded in the uteri of animals that have previously littered. Before the true nature of these bodies was discovered, more than one million sections were cut and examined.

All material was fixed with Zenker's fluid, and washed out with iodine alcohol. The paraffin bath was *in vacuo*—a most necessary precaution with such material. Sections are  $10\mu$  thick, and after dissolving the paraffin from the slide, they were cautiously coated with thin celloidin solution to prevent possible loss of such small objects as free ova or the loosening of membranes of older embryos.

Hæmatoxylin and eosin gave the best stain.

Free use was made of wax-plate reconstruction for verifying difficult points.

GRAF V. SPEE has already so fully described the normal non-pregnant uterus that it is unnecessary to go into a detailed description here. As in the human species, so also in *Cavia*, the uterine mucosa is divisible into two layers, the stratum compactum lying next the epithelium of the lumen, and the stratum spongiosum between it and the muscular coats. In *Cavia*, however, the lumen is slit-like and compressed laterally. A reconstruction of a perfect series of sections shows that it is also provided with little crypts or pockets in the anti-mesometric section of the lumen. These occur at varying distances throughout the greater part of the length of the uterus. This is a feature of great significance though it is not emphasised by GRAF V. SPEE.

#### THE FREE BLASTOCYST IN THE FIRST STAGE OF IMPLANTATION.

There are five examples of this phase in our series. One of them, 24 A, Plate I, fig. 1, is cut in an exceedingly fortunate plane, and is accordingly taken as the type for illustration and detailed description.

24 A, Age 5 Days. Dimensions, including Zona,  $0.072 \times 0.045$  mm.

As it is present in five sections, the third diameter must be about 0.05 mm. It lies nestling against the wall of a pocket in the anti-mesometric part of the uterus. The epithelium of the pocket next the embryo is thinned out and flattened, but otherwise shows no signs of departure from the normal condition. On the other hand, in the stratum compactum, not only in the immediate neighbourhood of the pocket, but around the whole anti-mesometric side of the uterus marked changes are taking place. The nuclei are more numerous, and many of them are of large size and of regular spherical form; the cell-bodies are more massive than elsewhere, and in consequence the whole area stains more deeply and presents a striking contrast to a corresponding part of the uterus where no embryo is present.

The position of the blastocyst in the pocket or crypt together with the associated changes in the stratum compactum are to be particularly noted as having a most important bearing on the subsequent stages.

Three cells from the discus proligerus are still attached to the embryo. The zona

\* "Early Development of *Cavia*; Note on Associated Remains of Previous Placentation," *Proc. Roy. Soc. Lond.*, B, vol. xcix, 1926.

radiata is very distinct. It is thinnest at the side next the epithelium, but nowhere shows signs of such breaking down as is to be seen in other embryos of this age.

The blastocyst cavity is clearly visible and surrounded by a single layer of cells, except at one side. Here there is a well-defined knot of cells which itself shows undoubted evidence of differentiation into two parts, an inner and an outer cell-mass.

The interpretation to be put upon the parts of this blastocyst is a matter of difficulty. At first sight one would conclude that the wall consists of trophoblast, and that this is thickened at one end to form the rudiment of the so-called *Träger* in the mouse or the rat; further, that the inner cell-mass represents the inner or formative cell-mass of classical descriptions. An examination of a full series of embryos, however, demonstrates, that while the polar thickening undoubtedly gives origin to the trophoblast of the *Träger*, the layer of cells bounding the cavity in the rest of its extent becomes directly converted into the lamella continuous with the definitive endoderm, and represents the endoderm of the inverted yolk-sac wall in mouse or rat. Thus the trophoblast instead of forming a layer which completely envelops the embryo as in the mouse or rat is in the guinea-pig localised at one pole only. The attenuated outer layer seen in these other rodents appears to be entirely suppressed in *Cavia*. Its presence has been assumed by most writers on the embryology of this animal, but it has never been actually observed. In spite of the most rigorous search, I have never been able to identify any layer of cells at any stage which could be supposed, even with a stretch of imagination, to represent this layer. It is therefore competent to conclude that it has been suppressed. As already stated, we do not know how this came about, as the immediately preceding phases have never been described. I hope to make good this gap in our knowledge, but meantime the sequence of embryos I have secured makes it evident (1) that the wall of the cavity of this blastocyst (which strictly does not deserve this name) consists of yolk-sac endoderm; (2) that the outer cell-mass constitutes the trophoblast; and (3) that the inner cell-mass represents the future amnio-embryonic ectoderm.

The cells seen projecting inwards in the figure are apparently endoderm cells that have come apart from the zona radiata. They are distinctly oval in contrast with the rounder cells of the knob. Two deeply stained flattened oblong nuclei are seen in the angles between the knob and the endoderm. They are very distinctive and differ from all other nuclei in the blastocyst, but their significance is not clear.

SECOND STAGE OF IMPLANTATION. DISAPPEARANCE OF THE EPITHELIAL WALL OF THE CRYPT.  
STRATUM COMPACTUM STILL INTACT.

Two embryos, 31 B 73 and 31 A 58, illustrating this phase, are seen in fig. 2, Plate I, and fig. 3, Plate II; also text-figs. 1 and 2.

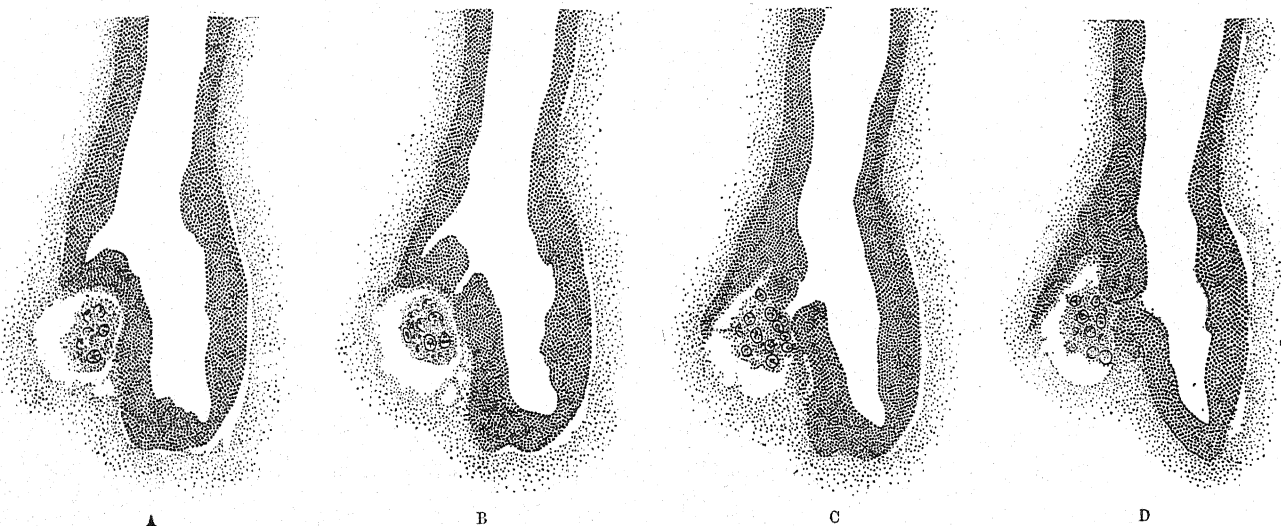
*Age 6 Days. Dimensions: 31 B 73,  $0.075 \times 0.055 \times 0.06$  mm.*

*31 A 58,  $0.079 \times 0.05 \times 0.05$  mm.*

Both of these embryos recall at once some of GRAF v. SPEE's illustrations, but some of the later figures of EMRYS-ROBERTS and of HERMANN and STOLPER are not so easily reconciled to them.

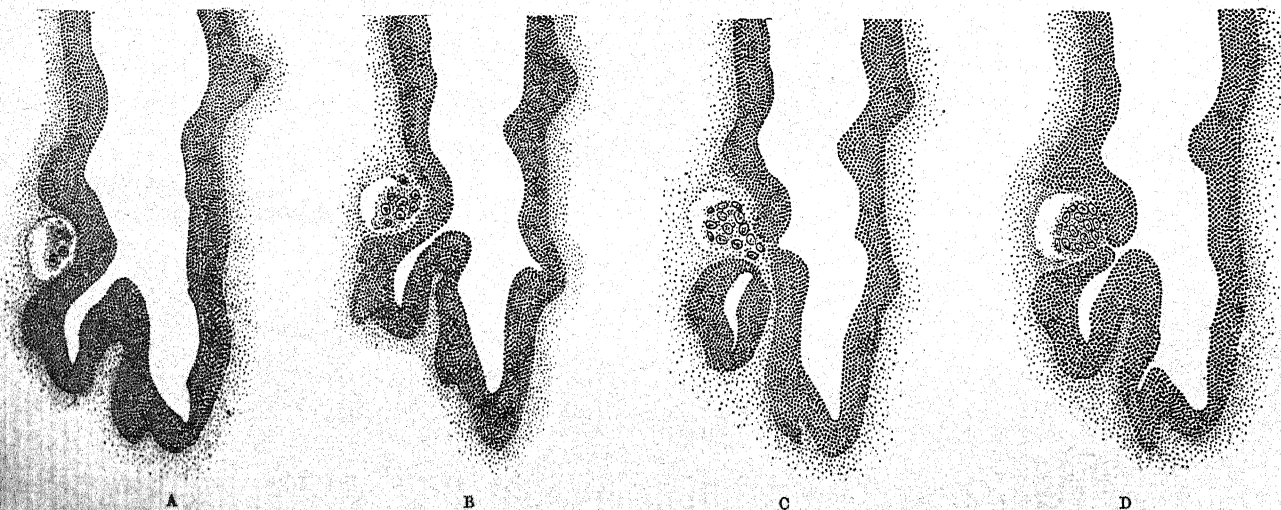
31 B 73 is apparently lodged in a nest which has been excavated below the uterine epithelium. The condition of the stratum compactum is similar to that in 24 A, but

brought to a much higher degree of development. The nuclei of the decidual cells are very large, of spherical form, and closely massed together. Mitotic figures are numerous. The cell-bodies are no longer sharply isolated from one another, but form what is practically a continuous protoplasmic matrix. The whole area involved takes on the hæmatoxylin



TEXT-FIG. 1.—Schematic drawings of four serial sections through the site of implantation of 31 B 73.

and eosin stain with a peculiar and very distinctive matt effect. At one side of the mouth of the crypt in which the embryo lies there extends a slip of degenerating epithelium between the embryo and the stratum compactum. At the opposite side from this slip there are seen a few cells which seem to be of the same nature. Both lips of



TEXT-FIG. 2.—Schematic drawings of four serial sections through the site of implantation of 31 A 58.

the mouth of the crypt have every appearance of active growth. The lips of the corresponding gap in 31 A 58 and the adjacent cells of the stratum compactum have grown so extensively that the entrance to a crypt is bridged over and partially blocked by them. This is seen very well in text-fig. 2.

We have then the embryo at this stage lodged in a crypt which still retains in part a



lining of epithelium, although this is now in process of degeneration. The remainder of the epithelial wall has disappeared, and the underlying tissue of the stratum compactum shows an early phase of the destructive process which becomes so pronounced in later stages. The decidua immediately round the crypt is practically nuclear-free. The matrix stains somewhat strongly with eosin, is very finely granular, and shows the beginning of vacuolation.

The presence of a partial epithelial lining in the crypt is an important feature. It cannot readily be explained on the hypothesis that the embryo has become implanted by boring its way through the epithelium. A more feasible explanation of the phenomena is that 31 B 73 was received into a crypt similar to the one in which 24 A is lying. The margins of that crypt then grew over the embryo, while the epithelium underneath degenerated. Older embryos, as we shall see, supply evidence in favour of this view. The peculiar position of 31 A 58 is explicable on the assumption that the crypt in which the embryo lodged was forked, as indeed these crypts frequently are.

In 31 B 73 the zona radiata is completely gone. The knob is now divided into two parts, trophoblastic (*Träger*) and central cell-mass (ectoderm), with the incipient extra-embryonic coelom lying between. The blastocyst is thus bipolar, and that part which represents the endoderm surrounds the pole opposite to that occupied by the localised trophoblast (*Träger*), while the original cavity of the blastocyst, as seen in 24 A, has completely disappeared. It is noteworthy that the trophoblast is already firmly adherent to the epithelium, while the endoderm, though doubtless during life in protoplasmic contact with the opposite wall, here shows a free margin. In both this embryo and 31 A 58, the nuclei of the endoderm cells show a tendency to be smaller and more oval than those of either trophoblast or central cell-mass.

### THIRD STAGE IN WHICH THE DESTRUCTION OF THE STRATUM COMPACTUM HAS COMMENCED, AND IMPLANTATION IS COMPLETE.

The rapidity with which these changes must take place can be realised by comparing the two embryos, 31 B 73 and 31 B 33. These two were in the same horn of the same uterus, and are only some 800 sections apart (about 8 mm.). Yet the period between the births of the young of *Cavia* at one litter cannot be very great.

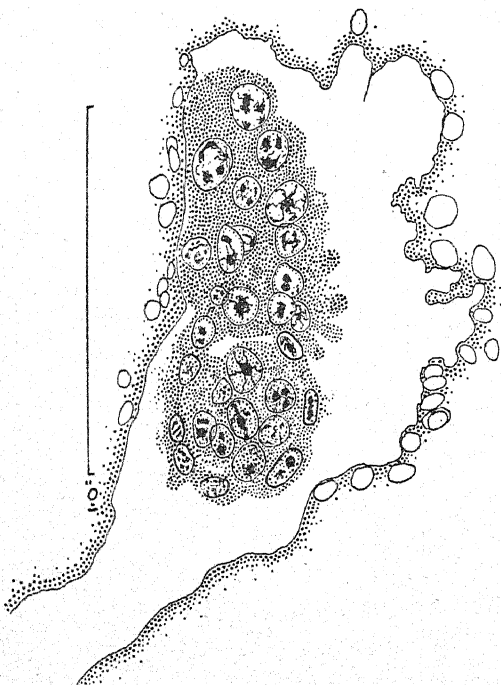
31 B 33. Age 6 Days. Length 0.11 mm. (Text-fig. 3.)

Unfortunately the plane of section is almost tangential to the uterine lumen. Hence, though extremely valuable for study, yet a single drawing or photograph illustrating at once the relations of embryo to epithelium and lumen cannot be got. Other embryos admit of this so admirably that observations on this specimen are confined to the embryo itself.

The embryo is attached to the under side of the epithelium at one side of the *Träger* only, the rest of its periphery lying apparently free in the space produced by the destruction of the stratum compactum. I say apparently, because tags of protoplasmic processes can be seen projecting from both the trophoblast and endoderm, and suggest that in life they might have extended across the destroyed area and been in contact with cells of the stratum compactum. The nuclei of the ectodermic knob, while heavily laden with chromatin, do not take hæmatoxylin quite so deeply as do those of the endoderm or trophoblast. The nuclei of the endoderm are distinctly oval. The space between ectodermic knob and the *Träger*—future extra-embryonic coelom—is clearly seen.

2 C 2. *Age uncertain. Dimensions*  $0.12 \times 0.057 \times 0.06$  mm. (Pl. II, fig. 4, and Pl. III, fig. 6.)

In this specimen the destructive process affecting the decidual tissue has become very active. The nuclei of the stratum compactum are now differentiated into two types. Those immediately surrounding the destruction space are relatively small, heavily charged with chromatin, and stain deeply, while the more distant ones are larger, clear, and vesicular, and the comparatively small chromatin content is distributed mainly over the nuclear wall.



TEXT-FIG. 3 — Embryo 31 B 33.

The result of this differentiation is the general appearance of an irregularly deeply-staining zone in the immediate vicinity of the embryo, with a paler zone beyond, as seen in fig. 6, Plate III, and fig. 4, Plate II. The destruction space is already larger and more irregular (fig. 6). This figure gives a general view of the embryo and its relations to the uterine lumen and destruction space. In the formation of this space it can be determined from this and other specimens of the same stage that both vessels and glands are involved in the breaking down of the tissue of the compactum. The most striking feature is the presence of certain plasmodial strands (fig. 6); one, smaller, immediately to the left of the embryo between it and the decidua, I take to represent the remains of the epithelial lining of the pocket in which the embryo lay previous to its implantation, while the larger mass of degenerating epithelium lying lower down in the specimen demonstrates how

the extreme anti-mesometric part of the uterine cavity has now become obliterated and its wall become involved in the destruction process.

The embryo has grown in length. The *Träger* is now a many-celled mass with no definite cavity as yet apparent in it. The nuclei are rounded and do not stain quite so deeply as those of the ectodermic knob. The nuclei of the endoderm are smaller and more oval; they stain somewhat differently from those of either the ectodermic knob or *Träger*. From some of their cell-bodies little processes of cytoplasm extend outwards. Between the *Träger* and the ectodermic knob is seen the still small extra-embryonic coelom.

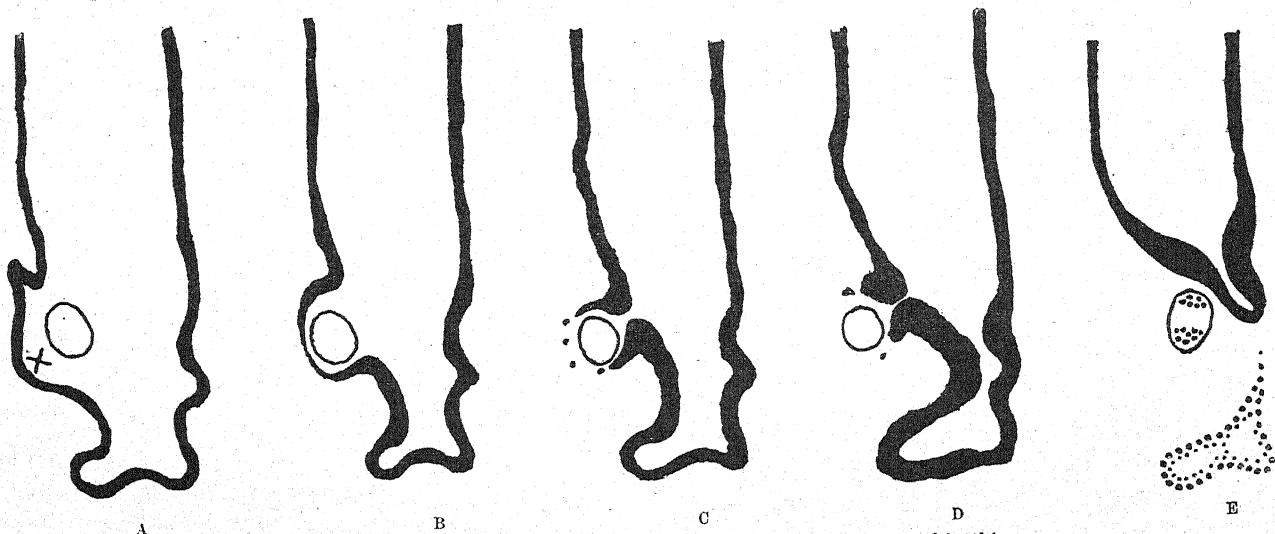
*Embryo 2 A. Age uncertain. Dimensions*  $0.16 \times 0.07 \times 0.07$  mm. (Pl. III., fig. 5.)

Though the exact age of this beautiful specimen is unknown, it is obviously older than 2 C 2. The destruction space here is still larger and more irregular. A strand of plasmodium, which I believe to be derived from the destroyed epithelium, is well seen occupying a similar relative position to embryo and cavity of uterus as in the previous figure. Of great interest is the small cavity seen in the uterine epithelium, the remnant of the anti-mesometric corner of the uterus in process of obliteration. The intimate relation of trophoblast to uterine epithelium is excellently seen. A new development is the appearance of a cavity in the *Träger*, the trophoblastic cavity, which in still later stages becomes so

very large and ultimately is concerned with the development of the placenta. The extra-embryonic coelom is also relatively larger, and in the actual specimen is seen to be lined by an exceedingly fine and apparently structureless membrane indicated in the figure, but not completely drawn in on account of its excessive thinness. As the blastocyst increases in size from this stage, the endodermic wall becomes relatively thinner, while the layer of endoderm immediately surrounding the ectodermic knob becomes thicker. The former in fact may be regarded as non-formative endoderm in contrast to the latter, which ultimately takes part in the formation of the gut.

#### SUMMARY AND CONCLUSIONS.

As was stated at the commencement of this paper, my object is to demonstrate a method of implantation as an alternative to that suggested by the theory of GRAF V. SPEE. Text-fig. 4 attempts to provide a diagrammatic recapitulation of the processes involved,



TEXT-FIG. 4. --Hypothetical figure of the process of implantation as interpreted in this paper.

according to my interpretation of them, in the stages we have now examined. A is an outline drawing of an actual uterus containing a free embryo (No. 24 B 18). This specimen was chosen because it possesses several crypts, in any one of which the embryo might have come to rest. I begin with the assumption that the embryo became lodged in the crypt X in diagram A; diagrams B, C, and D then represent successive phases of the process by which the embryo is finally implanted, as is shown in E.

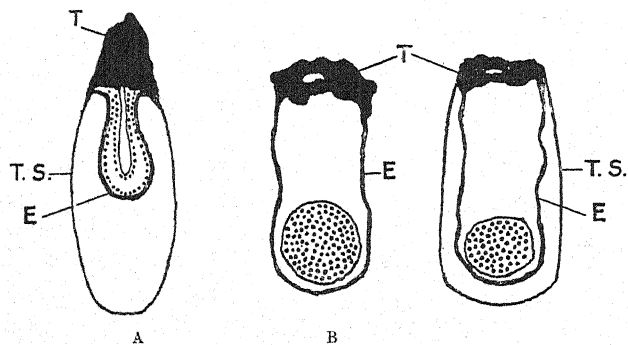
B corresponds in our series to 24 A, in which the embryo lies against the somewhat thinned-out epithelium at the bottom of a crypt whose lips have not yet commenced to enclose it. C corresponds to 31 B 73 where the lips of the crypt are grown together and almost meet, but a plug of trophoblast is still separating them. The epithelium of the crypt is still present at the sides (in 31 B 73 at one side only), but is obliterated at the bottom. D corresponds to 31 A 58 where the lips and trophoblast are in still more intimate relationship and the epithelium of the crypt is almost gone. In this diagram the lower lip is represented as projecting far into the anti-mesometric lumen. Exactly such a stage has not actually been observed, but from the analogy of 31 A 58 in which the epithelial lips have grown over and cut off a secondary crypt, it is believed that by a continuation of the



same process the lower lip comes in contact with the opposite wall of the uterus, and so cuts off the main anti-mesometric pocket. It is only in some such way as this that stage E can be realised. This diagram represents embryo 2 C 2 in which the lips are completely fused together and the anti-mesometric crypt is completely cut off. The epithelial mass shown by dotted lines represents the degenerated epithelium of the anti-mesometric crypt, and corresponds with the epithelial remains seen in fig. 6, Plate III, while the strand of plasmodium so well seen in 2 A (fig. 5, Pl. III) is of the same nature, though some of the small plasmodial masses may be derived from the degenerating stratum compactum.

Implantation, then, is excentric but not interstitial. The embryo does not penetrate the stratum compactum, but is, as it lies in the crypt, enveloped by folds of epithelium which shut it off in what is really a part of the cavity of the uterus.

The epithelium of the bottom of the crypt first disappears, then that of the whole anti-mesometric part of the uterus which lies at a lower level than the embryo. Finally the whole lumen is obliterated, but this occurs at a much later stage than any of those with which we are dealing here. The



TEXT-FIG. 5.—Diagrammatic representation of arrangement of trophoblast and endoderm in *Mus* and *Cavia*.

A, the condition in *Mus*; B, the actual condition in *Cavia*; C, the hitherto accepted idea of the condition in *Cavia* (Selenka); T, *Träger*; T.S., trophoblastic sac; E, endoderm.

primary process seems to be essentially one of circumvallation. One of the factors inspiring the researches on the early stages of development in *Cavia*, of which some of the results are recorded in the present paper, was the supposed close analogy between the process of implantation of the ovum in the human subject and that in *Cavia*. The ulterior stages of the process show extensive destruction of decidual tissue at the site of implantation in both cases. Regarding the primary stages involving the first absorption of uterine epithelium in the

human subject, it is of interest to note that the idea of circumvallation is a very old one, going back as it does to WILLIAM HUNTER.

SELENKA\* was responsible for figuring an enveloping sac of trophoblast for *Cavia* (text-fig. 5). DUVAL,† although he expressly says he did not work out the early stages of this animal, also assumed from the analogy of *Mus* that such an enveloping trophoblastic layer existed.

However, as has here been seen, no such sac exists in these stages, and certainly none is developed later. It is of great interest to observe that in *Cavia* the localised trophoblast or *Träger* forms indeed the "carrier," while the naked layer of endoderm is bathed by the contents of the destruction space.

I desire to express my deep sense of obligation to my chief, Professor BRYCE, for criticism and encouragement, and also and more especially for his kindness in embellishing my paper with the beautiful *natur-treu* figures—reproduced in Plates I and II. I must also thank Miss NIVEN, M.B., Ch.B., for her very excellent drawing reproduced on Plate III. Lastly, I desire to express my sincere thanks to the Carnegie Trust for the Scottish Universities for a grant in aid of the illustration of this paper.

\* *Studien u. Entw. d. Tiere*, 1883.

† "La Placenta des Rongeurs," *Journ. de l'Anat. et de la Physiologie*, 1892.

## DESCRIPTION OF PLATES.

(Wherever a scale occurs on a drawing it denotes 0.01 mm.)

## PLATE I.

Fig. 1. Embryo 24 A The embryo measures  $0.072 \times 0.045 \times 0.05$  mm., and occupies a crypt near the anti-mesometric end of the uterine lumen. The zona radiata is still intact. Three cells of the corona radiata survive, and the embryo consists of a vesicle, the wall of which is thickened at one pole. The thickening shows differentiation into an outer and an inner group of cells.

Fig. 2. Embryo 31 B 73. The embryo measures  $0.075 \times 0.055 \times 0.06$  mm. It occupies a recess formed by the overgrowth of the epithelial lips of the original crypt, the mouth of which is still open. The crypt is partially lined by epithelium which has, however, disappeared from the greater part of the floor. The decidual tissue is just beginning to show degenerative changes. The cavity of the embryonic vesicle has now disappeared. The interior is occupied by a solid mass of cells distinguished from the surface layer by slightly deeper staining and by the shape of the nuclei. The outer layer of the polar mass has established very intimate relations with the epithelium of the lips of the crypt.

## PLATE II.

Fig. 3. Embryo 31 A 58 The embryo measures  $0.079 \times 0.05 \times 0.05$  mm. In this specimen a crypt is seen originally placed distal to the original crypt of implantation. The decidual tissue bounding this latter crypt shows a further stage of vacuolation of the protoplasm. The trophoblast is seen extending into and involving the epithelium of a bridge that has cut off the secondary crypt from the lumen of the uterus.

Fig. 4. Embryo 2 C 2. The embryo measures  $0.12 \times 0.057 \times 0.06$  mm. The embryo lies free in the destruction space, with the upper part of the *Träger* in close contact with the uterine epithelium. Between trophoblastic mass and amnio-embryonic ectoderm lies the incipient extra-embryonic coelom. Note the epithelial remnant to the left of the embryo.

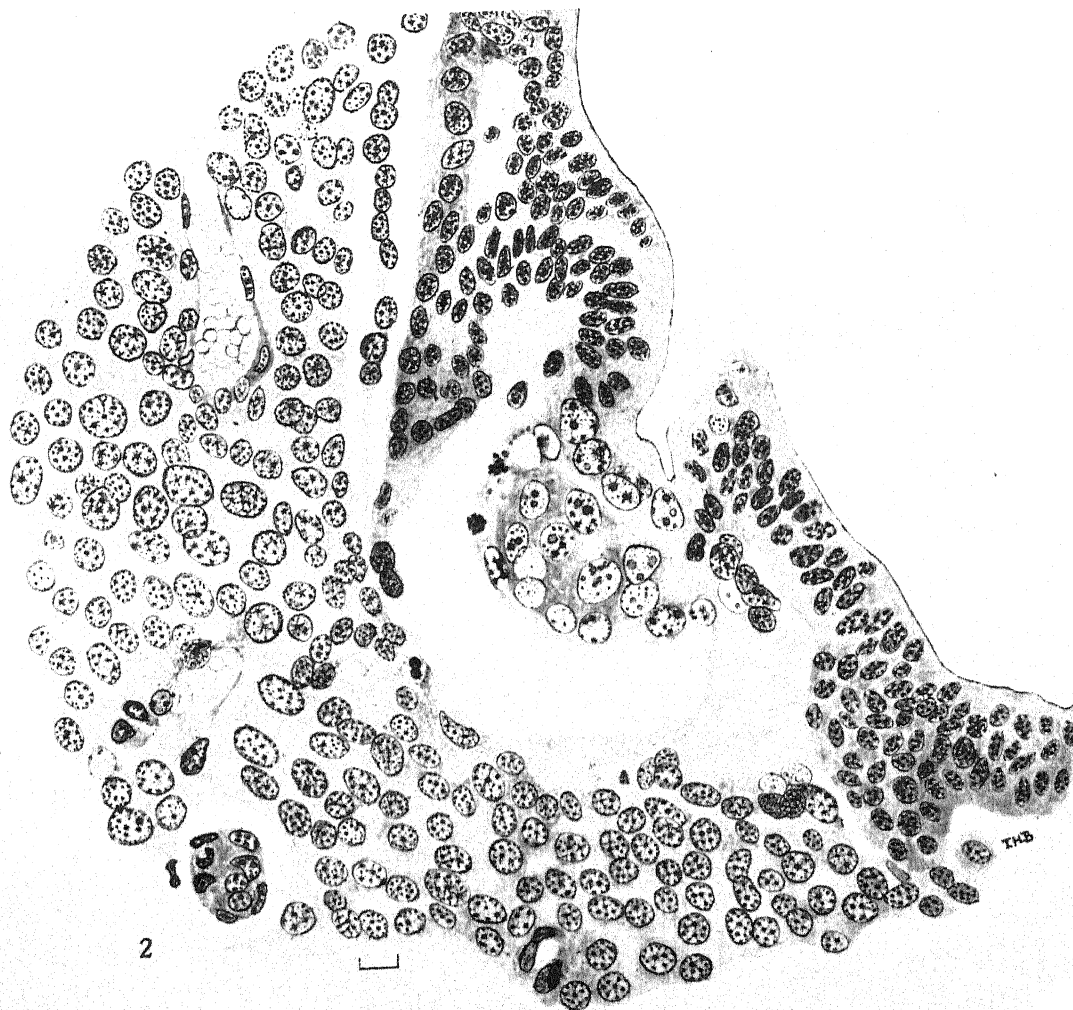
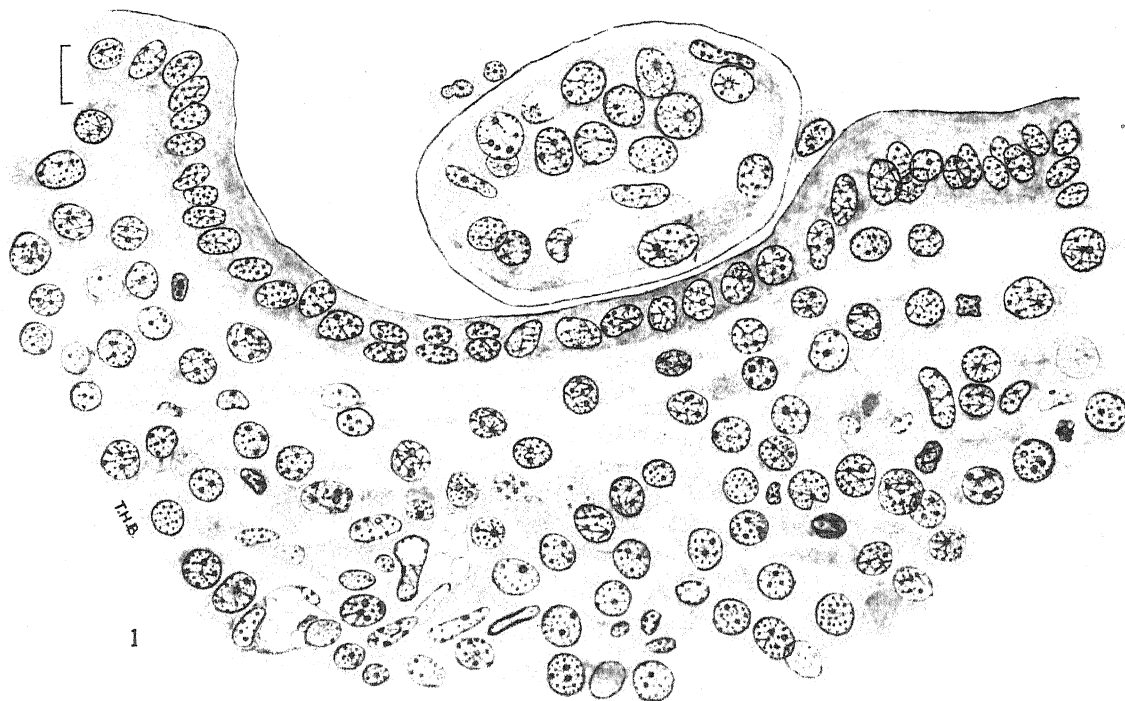
## PLATE III.

Fig. 5. Embryo 2 A. The embryo measures  $0.16 \times 0.07 \times 0.07$  mm. It shows clearly the cavity in the trophoblast (*Träger*) and the extra-embryonic coelom with its delicate lining membrane. The small cavity seen in the uterine epithelium to the left of the *Träger* is the all but obliterated anti-mesometric uterine lumen.

Fig. 6. Embryo 2 C 2. A photomicrograph of an adjacent section to that depicted in fig. 4. Two zones of the stratum compactum and the remnants of the epithelium of the anti-mesometric uterine lumen are clearly seen. The plasmodial mass seen has been alluded to in the text of the paper.

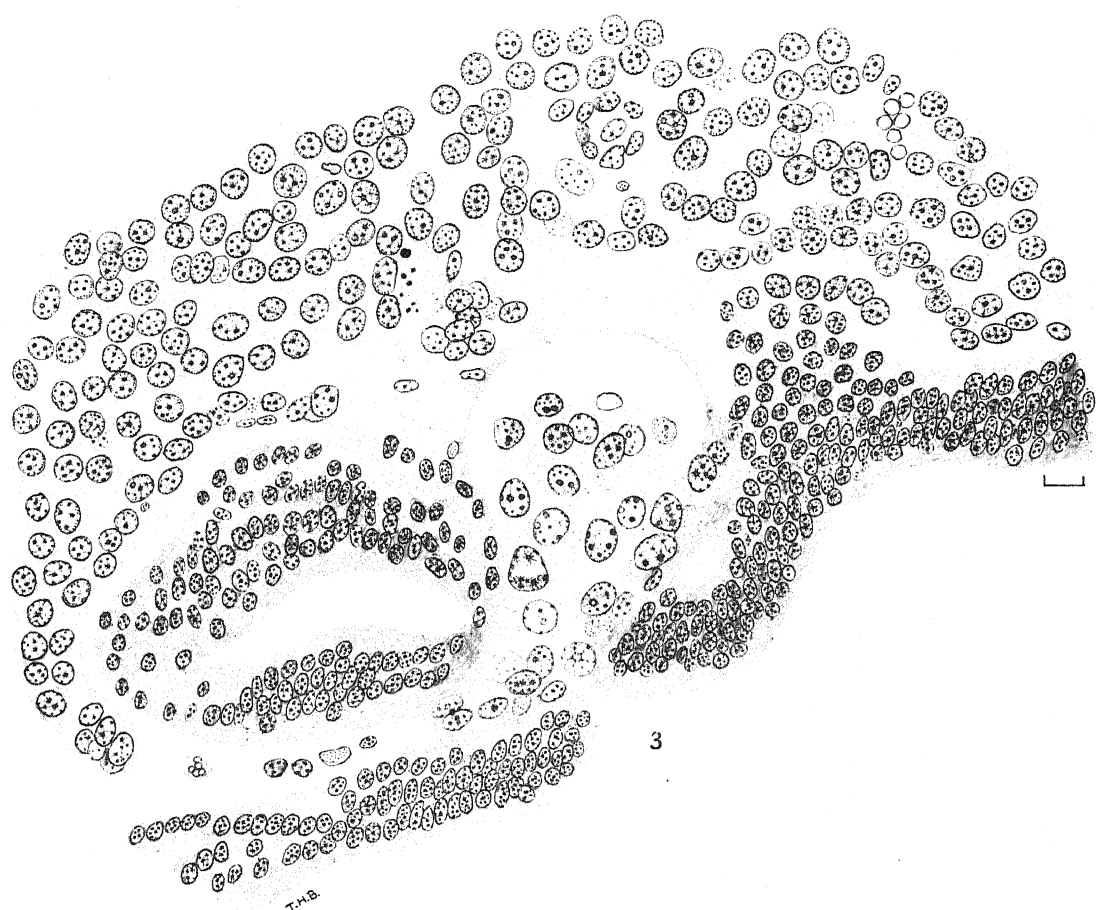








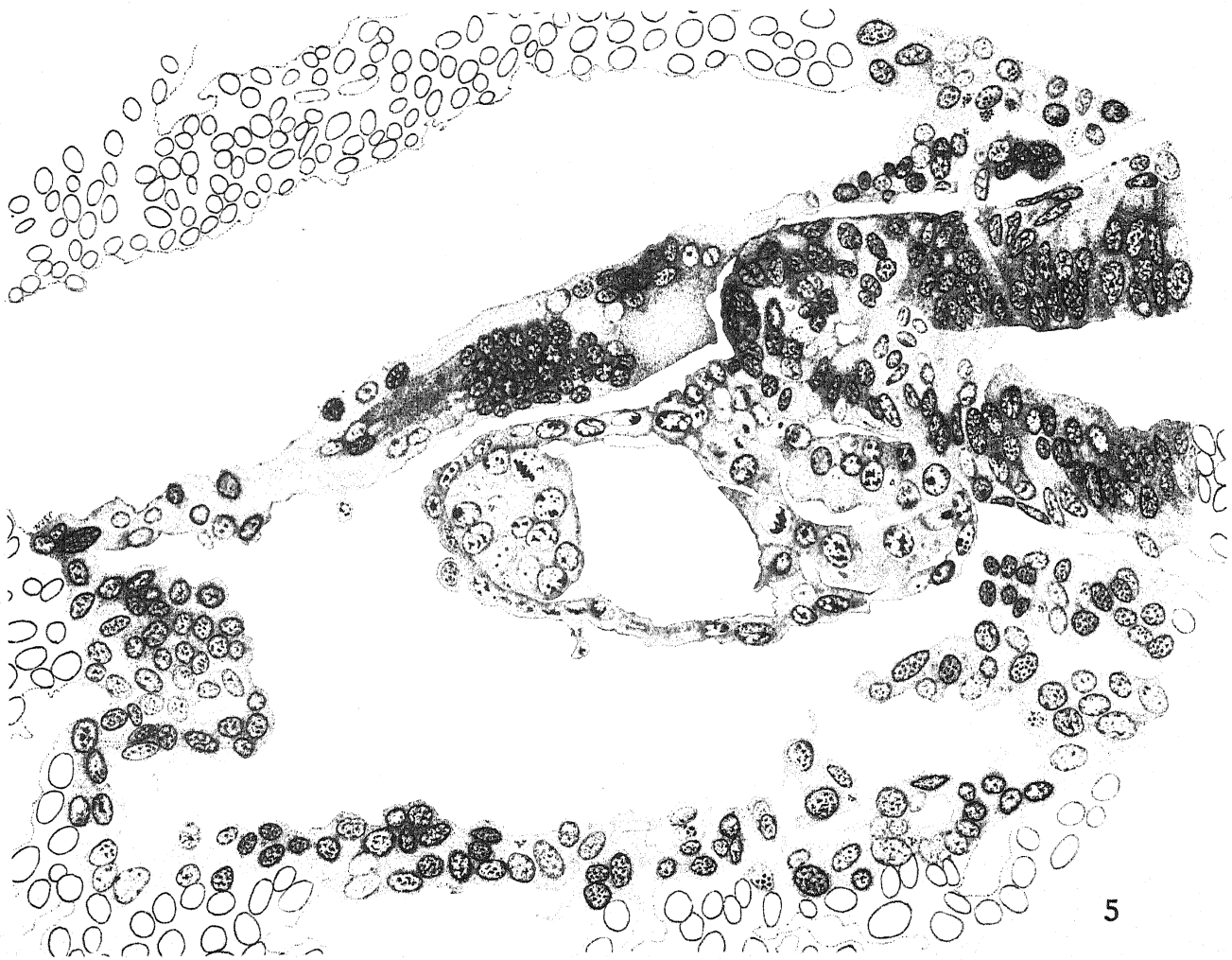
DR. N. MACLAREN—DEVELOPMENT OF CAVIA. IMPLANTATION.



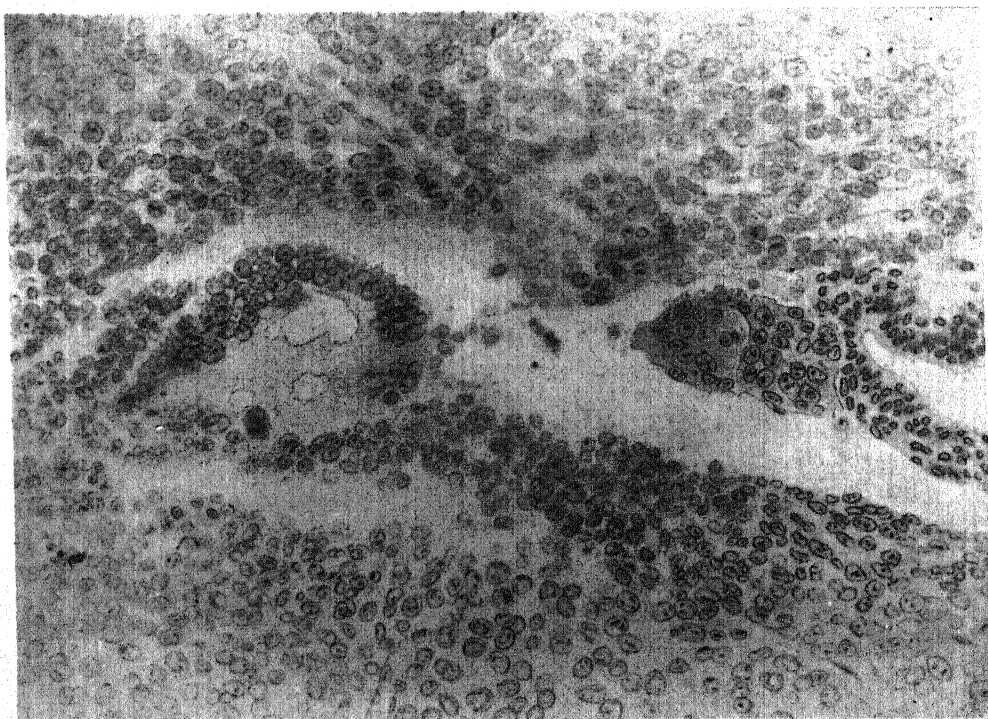




DR. N. MACLAREN—DEVELOPMENT OF CAVIA. IMPLANTATION.



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VI.—The Development of the Hypophysis Cerebri in Man, with a Note upon its Structure in the Human Adult. By David Waterston, M.D., Bute Professor of Anatomy in the University of St Andrews. (With Three Plates and Twelve Text-figures.)

(MS. received June 24, 1926. Read November 8, 1926. Issued separately December 13, 1926.)

The development of the hypophysis cerebri throughout the Vertebrates has attracted the attention of many workers, and our knowledge of its development and adult structure is comprehensive in many forms of the Reptilia, Amphibia, Fishes, in certain Marsupials, and in several of the best-known Mammals.

Its development in man has recently been investigated by RUDEL (1) and by HOCHSTETTER (12), but the small number of specimens as yet examined and described by these and other writers makes it desirable that further work should be done on this subject.

While in the general plan of its structure the human hypophysis resembles that of other Mammals—it is, for example, composed of an anterior or “oral” and of a posterior or “neural” lobe—the usual description of the adult mammalian hypophysis is not in all its details applicable to that of man. There is, for instance, in man no intraglandular cleft separating an anterior lobe proper from a “pars intermedia”; and a “pars intermedia,” as found in other forms, does not exist in the human adult gland.

The recent attention which has been given to the presence of a “pars tuberalis” in many forms renders it desirable that the presence and the development of this element in the human hypophysis should be investigated.

The purpose of the following paper is to describe a series of specimens of the development of the human hypophysis, and to discuss their bearing upon the structure of the adult organ.

A study of the developing hypophysis in *Tarsius* afforded some enlightenment on the condition in the human embryo, especially in connection with the morphological interpretation of what appeared to be the rudiment of a “lobus tuberalis.”

I have therefore included a description of a critical stage in the development of the gland in *Tarsius*.

Attention is drawn to certain features of the development of both the oral and neural lobes which have not hitherto been described, or have been incompletely dealt with; this, it is hoped, will throw light upon the structure and morphology of these parts in the adult organ.

It has been pointed out by other writers, and it has been very forcibly impressed upon myself, that in too many instances the development of the hypophysis has been described from sagittal sections alone, and frequently only from the appearance seen in a medial sagittal section, and that such material does not suffice to disclose the development and structure of the organ.

It is quite essential to supplement such material by the study of specimens cut in other planes and especially in the transverse, and several series of such sections have been used here.

## TERMINOLOGY.

It is necessary to define the terms used in describing the parts of the hypophysis, and it is desirable to employ terms which are applicable at all stages of their development. For this reason the terms "anterior" and "posterior" applied to the primary elements constituting the fully formed organ are here discarded, as they do not accurately represent the relative position of the two parts at all stages, and in place of them the terms "oral" and "neural" respectively are used.

The oral element originates as a transversely directed slit-like pocket from the roof of the stomodeum. The apex of the pocket is the ab-oral or distal end, while its mouth is the oral or proximal end. The slit is a transverse one, i.e. at right angles to the long axis of the embryo, and hence originally one surface of the pocket looks towards the tail end and the other to the head end. They are therefore here termed the "caudal" and the "rostral" surfaces respectively.

## DESCRIPTION OF INDIVIDUAL SPECIMENS.

*3-mm. Embryo. (2 W. 1.)*

The transverse sections of the head show in the roof of the stomodeum a small flat central area in which the oral epithelium is slightly evaginated, and lies in close relation to the wall of the diencephalon.

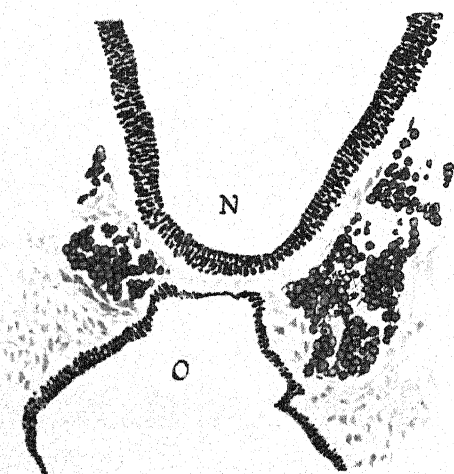


FIG. 1.—T.S. head of 3-mm. human embryo, showing the depression in the roof of the stomodeum.

N, neural tube; O, stomodeum.

The tissue on either side of the pocket is highly vascular. Fig. 1 shows one of the sections. It resembles a specimen described and figured by RUDEL (1) from a human embryo of about the fourth week. In his specimen there is a similar depression in the roof of the mouth cavity which he regarded as the beginning of Rathke's pocket. It is a single pocket immediately in front of the bucco-pharyngeal membrane, lined with low column epithelium.

The evagination is probably due to the neural wall and the oral epithelium retaining their original close proximity, while the growth of the maxillary processes, and the mesodermal thickenings associated with them, push the oral and neural walls apart from one another at the sides.

*6-mm. Embryo. (S. 1.)*

A reconstruction of the head at 100 diameters (not figured here) showed that the opening of the oral pocket is a transverse slit, slightly convex rostrally, lying opposite a recess in the floor of the mouth between the tuberculum impar behind and the mandibular arches in front. The rostral edge of the opening is sharp, while the caudal edge slopes gradually away into the roof of the mouth. The successive sections (fig. 2 (A), (B), and (C)) show that the recess is not merely a pocket-like evagination of the roof of the stomodeum.

The most anterior section, figured (A), shows a small chamber (V), which is continuous with the part O in the second figure (fig. 2, B), several sections further back. This section,

through the middle of the recess, shows a central stem, O, dividing into two horns which partially enclose the floor of the diencephalon. The most posterior section (C), again several sections back, shows the recess widening out, and gradually merging into the roof of the mouth cavity.

The apex of the recess in the median plane lies, separated by a layer of connective tissue, close to the floor of the diencephalon. On each side the oral pocket is prolonged into a lateral horn of considerable size, the two horns embracing the sharp ventral border of the neural tube (fig. 2, B).

The lining epithelium consists of long narrow cells set vertically to the surface.

No trace of the formation of a neural lobe could be detected in the floor of the diencephalon.

This condition of Rathke's pocket—a central stalk with two lateral horns—does not appear to have been hitherto recognised in the human embryo. WOERDEMAN figures a series of sections somewhat similar in the developing hypophysis in a mouse of 8.1 mm. length, and HOCHSTETTER's fig. 20 (*loc. cit.*, Tafel VI) shows a similar, but earlier, condition of a central

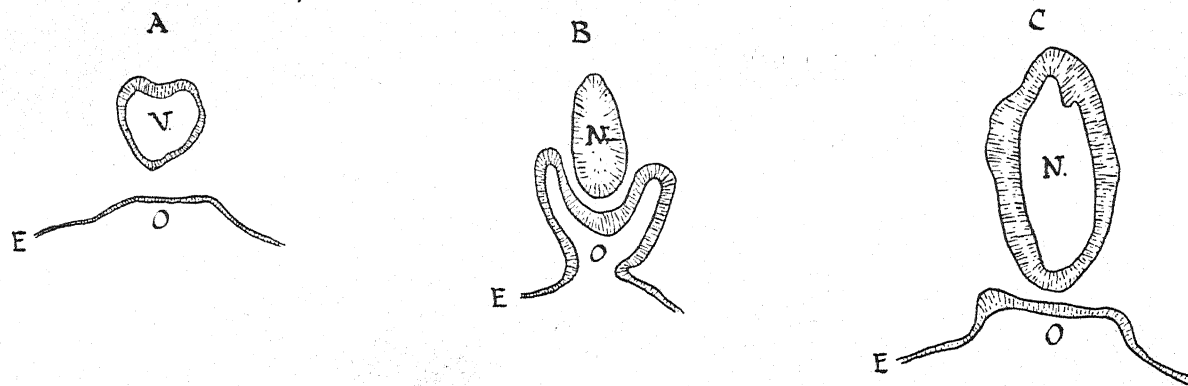


FIG. 2.—Tracings of transverse sections of hypophyseal region of 6-mm. human embryo.

A, the most rostral; B, four sections caudal to A; and C, four sections caudal to B. (Sections  $10\mu$ .) B shows the two lateral processes from the oral pocket which at this stage enclose the floor of the diencephalon.

O, oral pocket; E, epithelium of oral cavity; N, neural tube; V, "Vor-raum," continuous with the cavity O.

stem and two slight lateral recesses in a human embryo 8.13 mm. in length, but this has not attracted his attention. The rostral recess (fig. 2, A) is of considerable interest, for it demonstrates the occurrence, in a human embryo of this stage, of the rostral prolongation of the oral pocket, known as the "Vor-raum," to which WOERDEMAN ascribes considerable significance in his comparison of the development of the oral lobe of the hypophysis in Selachians, Reptiles, and in Mammals.

#### 8-mm. Embryo. (Figs. 3, 4, 5, and 6.)

The reconstruction (X-100) shows the oral pocket, roof of the mouth of pharynx, and the adjacent part of the neural wall.

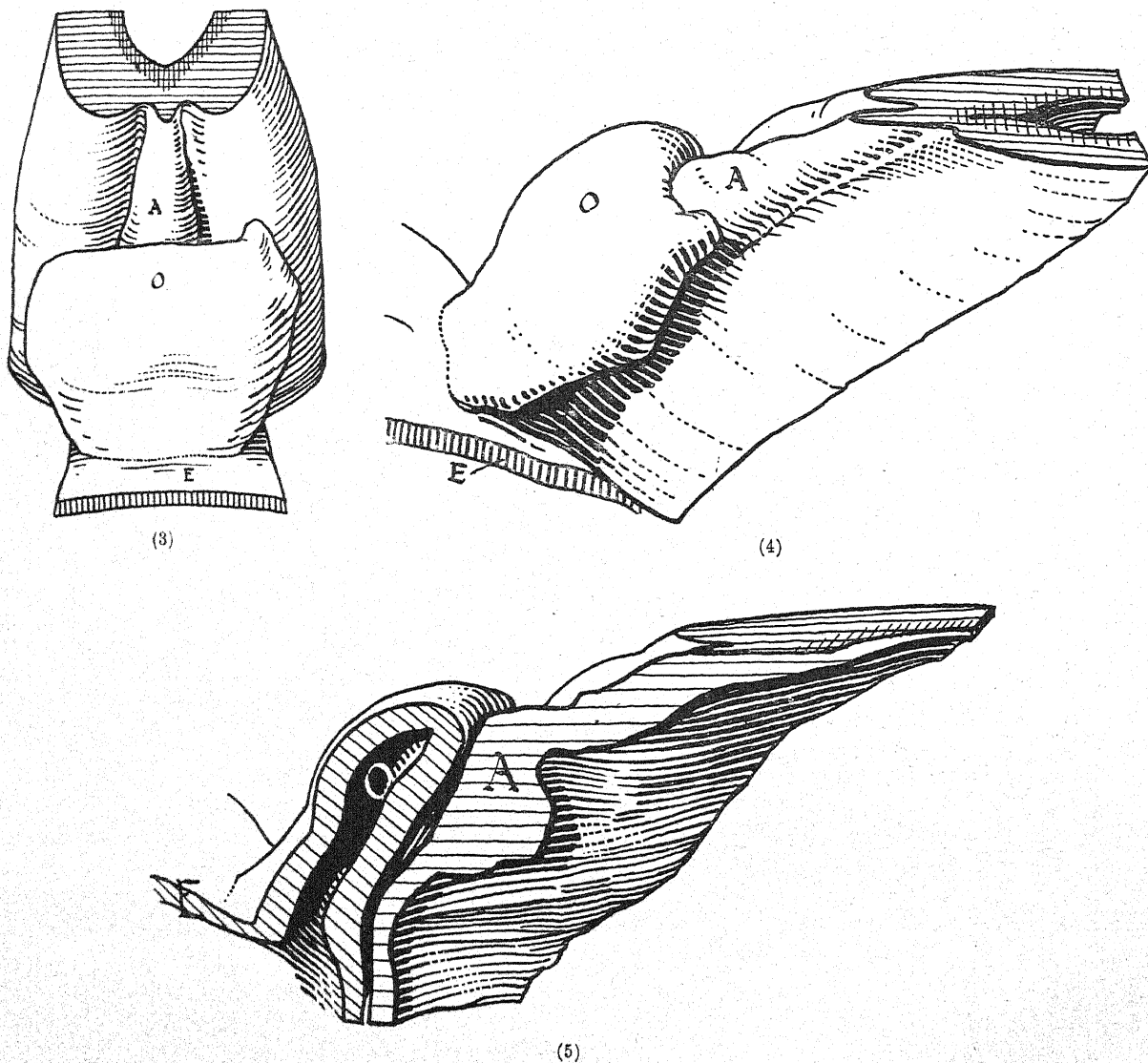
The orifice of the pocket in the roof of the mouth is a transverse curved slit, convex rostrally, limited by a sharp caudal margin, while the rostral wall slopes gradually into the roof of the mouth.

The pocket in the reconstruction is 45 mm. deep, 65 mm. in the coronal plane, and 16 mm. in the sagittal. In size, shape, and proportion it is similar to HOCHSTETTER's (12) reconstruction for an embryo 8.13 mm. in length (*loc. cit.*, Tafel V, fig. 7).



The transverse diameter of the pocket is narrowed at its root, the distal end is slightly concave, and the rostral surface is in close apposition in its whole length with the floor of the diencephalon.

This stage shows the early changes in the floor of the diencephalon which lead to the development of the neural lobe.



FIGS. 3, 4, and 5.—Wax-plate reconstruction of the hypophysis and adjacent neural tube in an 8-mm. human embryo. (3) Caudal aspect; (4) from the right side; (5) median sagittal section. Magnification of the model, 100 diameters, reduced by one-third in (3).

A, ridge of neural floor; O, oral pocket; E, epithelium of oral cavity and pharynx.

The sagittal medial section of the model figured in fig. 5 shows in the floor-plate of the diencephalon an area of thickening opposite the distal half of the oral pocket, bulging on the surface and into the cavity of the neural tube.

The lateral view of the reconstruction shows that the most prominent external part of this ridge (A) projects towards the recess on the distal border of the oral pocket. The transverse sections show that the neural lobe is not merely an evagination from the neural wall, and that it is only one result of extensive changes in the floor of the neural lobe.

Tracing the arrangement from the more caudal portion of the neural tube rostrally (fig. 6, A and B) there is first seen a single median pear-shaped projection (R) on the external surface of the tube, for the most part solid, but hollow at its root. It is composed of tissue similar to the inner ependymal layer of the neural wall.

More rostrally this median pocket presents two lateral evaginations from the neural cavity, separated from one another internally by a slight median ridge (C and D, fig. 6).

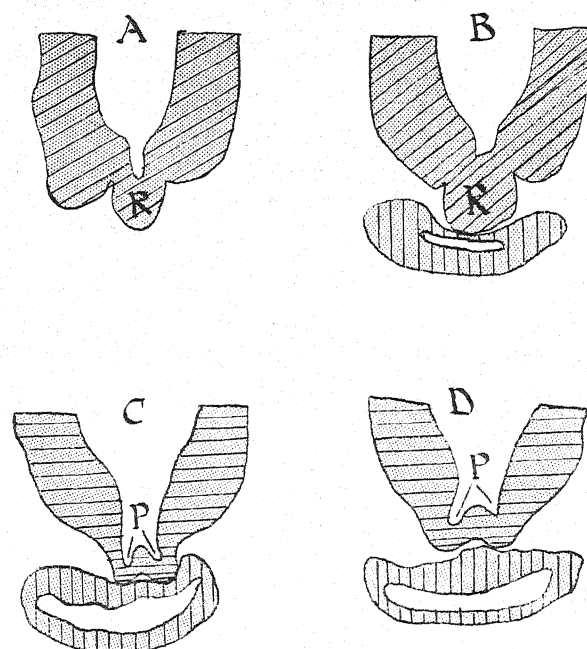


FIG. 6.—Four tracings of transverse sections of head of 8-mm. embryo. A, the most caudal; D, the most rostral, successive figures six sections apart.  
R, neural ridge; P, lateral neural pockets.

This arrangement persists through some ten sections. The pockets become less distinct on the external surface, but from the interior they remain very distinct, separated by a sharp-pointed crest.

The adjacent connective tissue is notably vascular.

A few sections further forward the pockets disappear and also the central thickening of the floor of the neural tube. The significance of these pockets is discussed later on (p. 142).

#### 10-mm. Embryo.

The sections of this specimen were in the sagittal plane, and fig. 7 shows a drawing from one of them, slightly paramedian. At a magnification of 100 diameters the oral pocket measures 64 mm. in length and 69 mm. in transverse width. Sections in the sagittal plane do not so clearly demonstrate the presence in the floor of the diencephalon of the lateral pouches described in the 8-mm. embryo, but they can be identified here also, and except for a slight increase in size, the specimen shows a condition similar to that in the 8-mm. embryo, and it does not require further description.

12.5-mm. Embryo. (Text-figs. 8, 9, and 10, and Plate I, fig. 1.)

In a plate reconstruction at 100 diameters magnification the general shape and arrangement of the oral and neural portions are shown. The oral pocket is similar to HOCHSTETTER'S

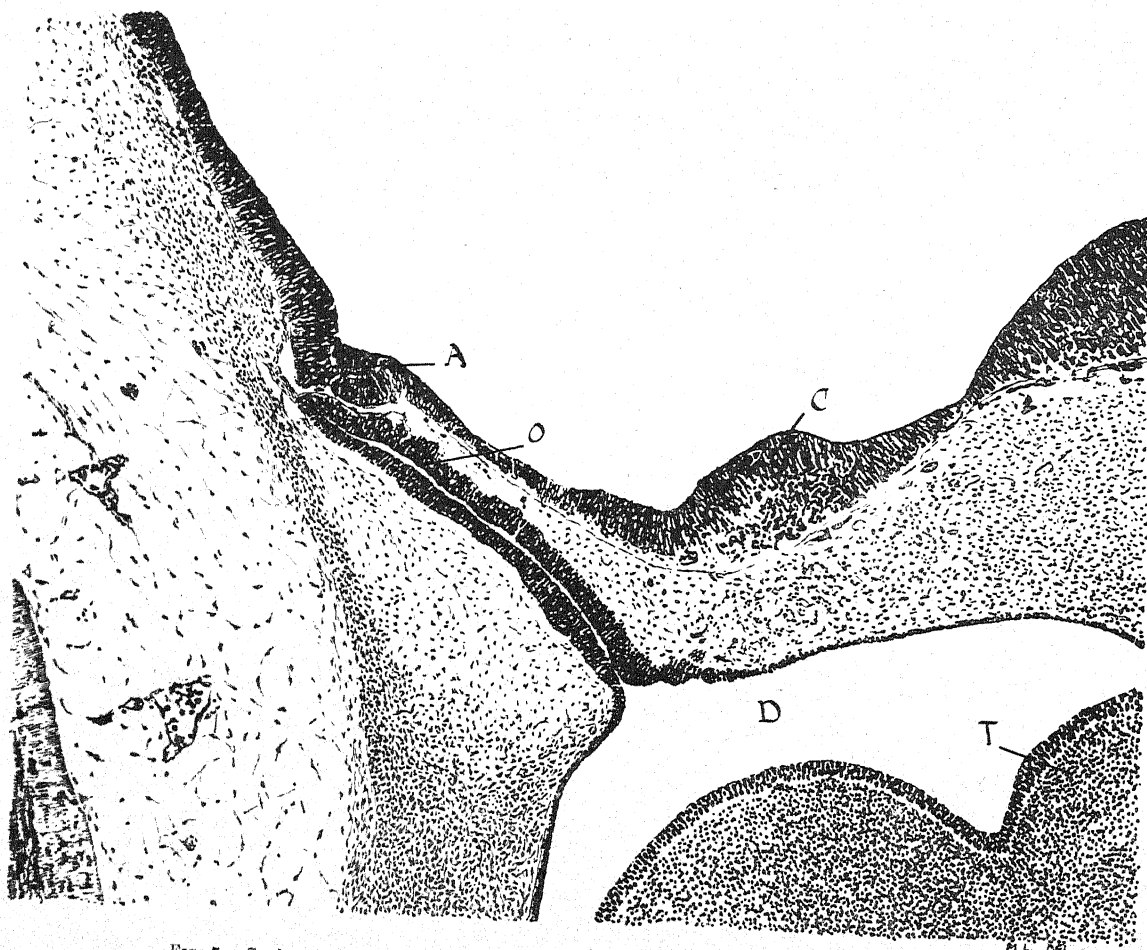
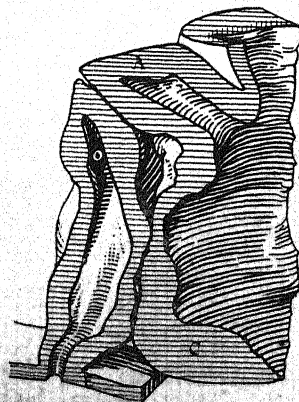


FIG. 7.—Sagittal section of head of 10-mm. human embryo; nasal end to the right.  $\times 100$ .  
A, infundibular thickening of neural wall; O, oral pocket; C, optic chiasma; D, oral cavity; T, elevation of tongue.



FIGS. 8 and 9.—Wax-plate reconstruction of the hypophysis and adjacent neural tube from a 12.5-mm. human embryo.  
Magnification, 100 diameters, reduced here by half.

A, infundibulum; O, oral pocket; E, epithelium; C, chiasma.



reconstruction from an embryo of 12.88 mm. in length, and consists of a slender tapering stalk, which opens into the oral cavity by a minute orifice, merely a fine sagittal slit, and

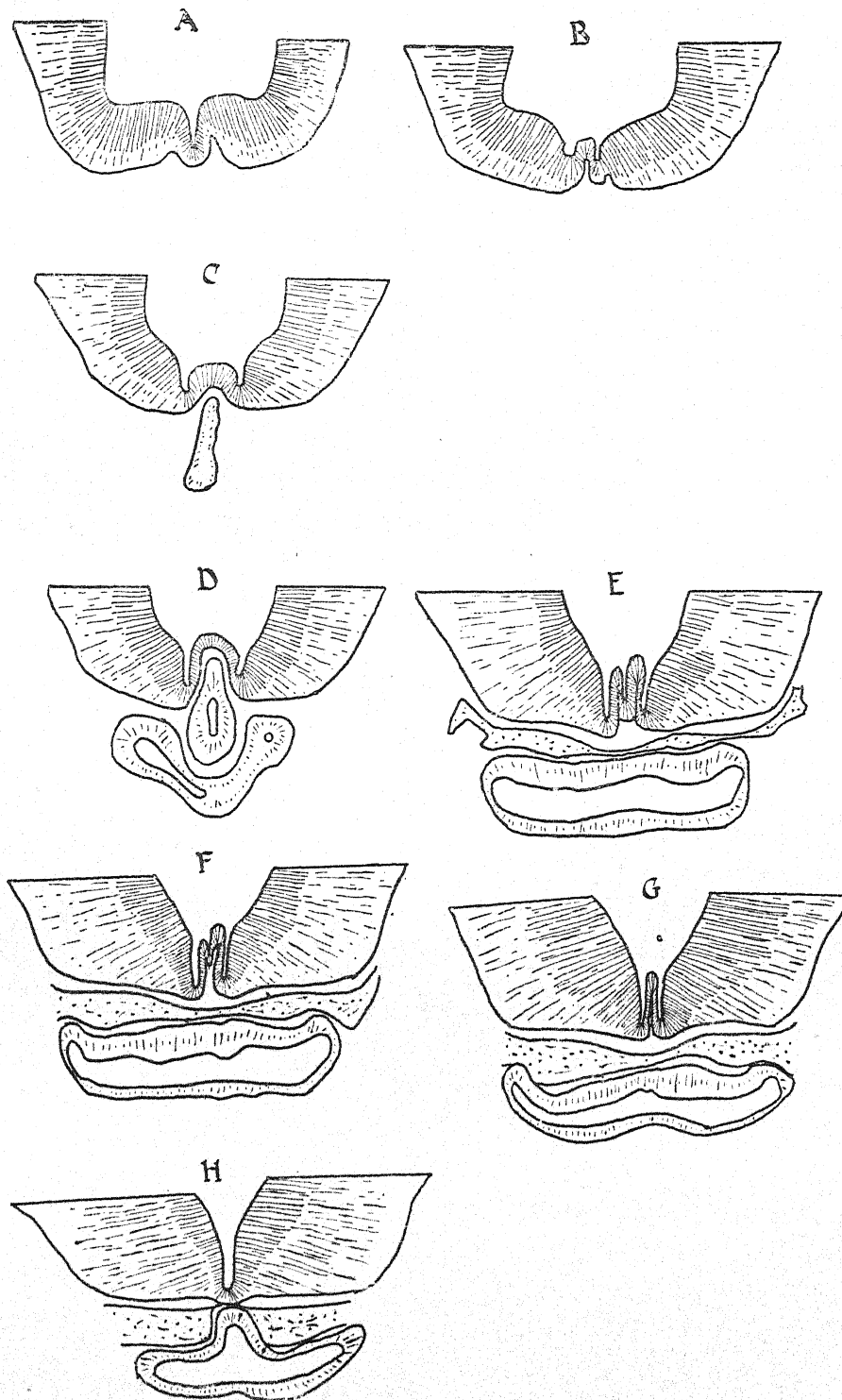


FIG. 10.—Tracings of successive sections, ten sections apart, of head of 12.5-mm. embryo. A, the most rostral; H, the most caudal, showing the lateral neural pockets and their relation to the infundibular process. (Sections  $10\mu$ .)  $\times 50$ .

of an expanded distal part. The root of the stalk passes on to the rostral surface of the distal "glandular" part and forms on it a projecting ridge. A transverse section shows a

triradiate lumen present in this region. The tubular portion of the stalk measures in the reconstruction some 13 mm. in length, and lies in the condensed pre-cartilaginous tissue of the cranial base. The expanded distal portion is leaf-shaped, tapering to the stalk. Its distal border is notched for the neural lobe, and the lateral margins are turned forwards and slightly lobulated. It measures in the reconstruction 55 mm. in height, apart from the stalk, and 80 mm. in width.

*Neural Lobe.*—The neural pocket projects from the floor of the diencephalon as a conical pointed process, having its root opposite the apex of the oral pocket, and projecting back into the groove on its distal border.

The floor of the diencephalon near the root of this lobe shows a highly complex degree of folding which would be unintelligible but for the simpler condition shown in the 8-mm. embryo. The reconstruction and the tracings of successive sections (text-fig. 10) show in the floor of the diencephalon a longitudinal median internal ridge almost 50 mm. long in the reconstruction, tapering at each end, and extending caudally and rostrally considerably beyond the limits of the outgrowths seen on the external surface.

The opening of the cavity of the neural pocket lies about the centre of this ridge and is directed slightly to the left side. Its cavity is continued into the end of the pocket, its outline irregular (Pl. I, fig. 2).

On each side of the ridge, examining from the interior, is a slit-like groove deepest at, and rostral to, the orifice of the evagination.

These grooves are clearly the same as the grooves noted in the 8-mm. embryo, but they do not in this specimen project as elevations on the external surface.

In the successive sections traced in fig. 10 is shown the arrangement at different levels.

In A, most caudally, is seen the rounded external projection from the floor of the diencephalon.

In B and C the folded crest in the interior of the neural tube.

In E the orifice of the neural outgrowth, directed slightly to the left, in the centre of the ridge, and the two lateral slits upon either side.

F, G, and H shows the gradual disappearance of the ridge. This convoluted arrangement of the floor of the diencephalon has not hitherto been described.

The condition is not an artifact, for the histological state of the embryo was practically perfect. Comparison with the 8-mm. embryo shows that the arrangement is the same—in the floor of the neural tube a ridge centrally and a recess on either side, with the opening of the "neural lobe" in the centre of the ridge.

#### 16-mm. Embryo.

The condition in the specimen is similar to that in the last, but the lateral margins of the oral lobe are more folded forwards.

There is the same projection of the root of the stalk on the rostral surface of the glandular portion.

The lumen, however, is no longer triradiate, for the lateral surfaces of the ridge are largely fused with one another, and the cavity obliterated.

In the floor of the diencephalon there are two small lateral recesses by the side of the neural outgrowth, similar to these in the former specimen, but less distinct, as the folding of the floor is much less in amount.

*Embryo 20 mm. in length (S 3).*

Plate I, fig. 3, shows a reconstruction at fifty diameters of the hypophysis viewed from the front, without the stalk.

The reconstruction of the oral pocket is similar to HOCHSTETTER'S (12) from an embryo 20.9 mm. in length (*loc. cit.*, Tafel VI, fig. 15). The stalk is a slender column of cells for the most part solid, the cavity having disappeared in the upper and middle parts, but is present at the lower, *i.e.* at the pharyngeal end. The stalk is embedded in the cartilaginous basis cranii, and measures in the reconstruction 64 mm. in length. At its distal end it passes into the border of the expanded glandular part. This distal glandular portion of the epithelial oral pouch is widely expanded transversely, measuring in the reconstruction 65 mm. in its maximum transverse width, and 37 mm. in length.

The form of its rostral surface requires careful examination, for it represents features which become of considerable importance later.

The rostral wall and the margins of this, the distal part of the primitive oral pocket, are the basis from which the "anterior lobe" of the adult hypophysis is formed, but all parts of this rostral wall do not participate alike, and all parts of its surface do not develop equally.

The principal parts showing rapid development are :

- (1) The lateral margins.
- (2) A ridge on the central part of the rostral surface.
- (3) The proximal margin.

The rostral surface shows a central crest, and the lateral and proximal margins curl towards it, producing on each side of the central projection a deep hollow filled with connective tissue.

The distal border shows a central depression in which lay the stalk of the neural lobe; eventually this stalk becomes enclosed by the lateral horn-like projections.

Sections of the various portions of the body show a large lumen in each of the horns and in the body; the bending forwards of the lateral margins; and nodular thickening of the anterior wall through the formation of solid ball-like masses of cells. In the wall of the right horn is a large well-formed follicle.

The turned-up proximal margin is rounded and lobulated except in its central portion, which at this stage remains flat, and marked by a rounded projecting ridge which extends forwards on the rostral surface (Pl. I, fig. 3).

The neural lobe has a short thick stalk, compressed from side to side, and with a wide lumen lying between the lateral horns of the buccal portion. The apical portion is widened out and lies in contact with the caudal surface of the body of the oral lobe for some 15 ( $\times 50$ ) millimetres. The tissue of the neural lobe is continuous with the ependymal lining of the central canal of the neural tube. The floor of the tube is not convoluted as in the 12.5 specimens, but at the root of the infundibulum there are slight lateral pouches. These pouches extend beyond the root of the infundibulum, both rostrally and caudally.

Rostral to the root of the infundibulum, the floor of the third ventricle projects from the surface of the neural tube and forms a flat plate in contact with the rostral surface of the oral lobe.

The significance of this is quite obscure, and has not been noticed in any earlier specimens, but occurs also in a 26-mm. embryo.



Other embryos of a stage of development similar to S. 3 were examined, but are not figured. These included embryos LL, PP, and NN of Professor Bolk's collection, of 20 mm., 21 mm., and 22 mm. length respectively.

The condition in each was like that described here, and individual description is unnecessary. In particular, in each, the oral lobe showed a central ridge projecting from the lower part of the rostral surface, and an upturned lower margin, though in "PP" the crest was less well marked than in the other specimens.

*26-mm. Embryo, E 1. (Pl. I, fig. 4.)*

The model of this specimen viewed from behind recalls in its general form the adult hypophysis. There is an expanded oral lobe, measuring in the reconstruction (at 50 diameters magnification) 67 mm. in transverse width, 30 mm. in vertical height, while on each side from the upper border horn-like conical projections extend 30 mm. upwards by the side of the stalk of the neural lobe (infundibulum). The neural lobe is roughly pear-shaped, lies in a groove on the distal part of the buccal lobe, and has a short and wide stem connecting it to the floor of the third ventricle. The central cavity of this lobe is very slender and is obliterated in the stalk, reappearing irregularly in occasional sections lower down.

*Oral Lobe.*—The rostral surface of the oral pouch shows a further degree of development.

The lateral margins (Pl. I, fig. 4, 2) are more turned inwards and the proximal margin (Pl. I, fig. 4, 3) turned upwards. There is a nodular growth from the central part of the rostral surface, and the lateral hollows on each side filled with connective tissue are more pronounced.

The cavity of the buccal lobe is for the most part large and wide, but it is partly obliterated by fusion of the opposite side in these portions of the lobe which are bent forwards. The caudal wall of the cavity consists of a thin layer of epithelium thickened where it is in contact with the neural lobe. Below the apex of the neural lobe it is thin.

Horizontal sections of the proximal part of the oral lobe show thickening of the rostral wall and a proliferation of epithelial buds. In the lowest part this proliferation has the form of a T-shaped mass, a stem springing from the middle of the rostral wall of the epithelial cavity, and the cross limb of the T is a wide extension of lobulated epithelial tissue extending on each side as far as to the margins of the infolded lateral masses. Numerous follicles are evident in this portion.

Elsewhere the lateral margins are largely solid and are connected to one another across the middle line by a thin lobulated cord of gland tissue, the upper margin of the upturned lamina.

This cord is connected in the middle line to the crest on the rostral surface, and hence on each side is a pocket in which is a quantity of connective tissue. This pocket extends laterally into the hollow formed by the bending forwards and medially of the lateral masses.

*30-mm. Embryo. (Pl. I, fig. 5.)*

In the reconstruction of this at 50 diameters enlargement the transverse width is 75 mm., the height of the oral lobe in the middle line is 23 mm., and its sagittal diameter 16 mm. In its proportions it differs from those of former specimens, but the general form is the same.

The oral lobe is widely expanded transversely, the lateral margins are incurved and highly lobulated, and thickened at their extremities. The stalk has disappeared. The distal margin is deeply notched at the centre, forming a semicircular recess in which lay the neck

of the neural lobe. The neural lobe, pyriform in outline, extended downwards from this notch on the caudal surface of the glandular part.

The proximal margin of the oral lobe is curved forwards and dorsally, forming a narrow lobulated band stretching across from one lateral margin to the other.

There is again a distinct median crest, projecting forwards from the centre of the rostral wall to the upcurved lower edge.

The model shows an appearance intermediate between the specimens from a 25-mm. and from a 41-mm. embryo figured by HOCHSTETTER (Tafel VI, figs. 17 and 18).

The figure (Pl. I, fig. 5) shows the condition of the rostral surface with the thin lamina

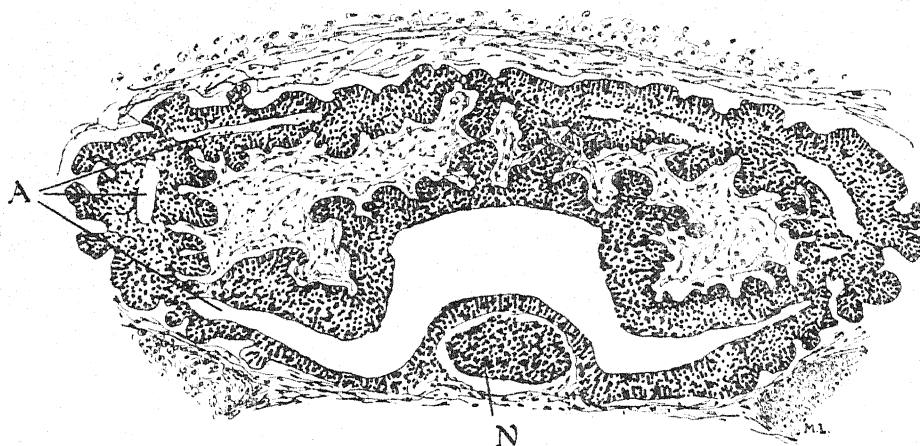


FIG. 11.—T.S. 30-mm. human embryo. Showing the partial obliteration in front and at the sides of the intra-glandular cleft, the central mass, the anterior lamina, and the lateral masses.

A, intra-glandular cleft; N, neural lobe.

formed from the lower margin stretching across from one side to the other and attached to the central ridge.

The figure also shows the deep lateral recesses on the rostral surface formed by the curving forwards of the margins. These contain connective tissue, which later on is almost completely enclosed by gland tissue.

#### 40-mm. Embryo, R. R. (Professor Bolk's Collection, Sagittal Sections.)

The figure (text-fig. 12) shows the increase in size of the process which has grown from the proximal margin, for it now reaches almost to the floor of the neural tube (tuber cinereum).

In the section figured the "central mass" is smaller than in the younger and in the older embryos. Comparison of this with a section of an embryo of the same length (Bryce collection) shows the amount of individual variation which may occur, for in this latter specimen the central mass is relatively very large.

#### 50-mm. Embryo. (Bryce Collection.)

In this specimen the same parts are present, they are more compressed together, but show no material difference from the condition in the former embryo of 30 mm.

*Tarsius Embryo.* Hubrecht Collection, No. 72. (Pl. II, figs. 6 and 7.)

A reconstruction of the hypophysis was made at a magnification of 66 diameters, and in it the hypophysis measures 33 mm. transversely and 26 mm. in vertical height.

The fig. 6 (Pl. II) shows the general shape.

The neural lobe is attached by a rather thick stalk to the floor of the diencephalon. The oral lobe is completely cut off from the mouth cavity.

There are several distinct differences between this specimen and human specimens of approximately the same stage of development (25 to 30 mm.) as well as older and adult human hypophyses. The neural lobe does not, as in man, lie in a recess on the caudal wall of the oral lobe, but invaginates the distal part of this surface and comes to be completely surrounded by the oral epithelium. Transverse sections show the neural lobe as a solid cylindrical mass

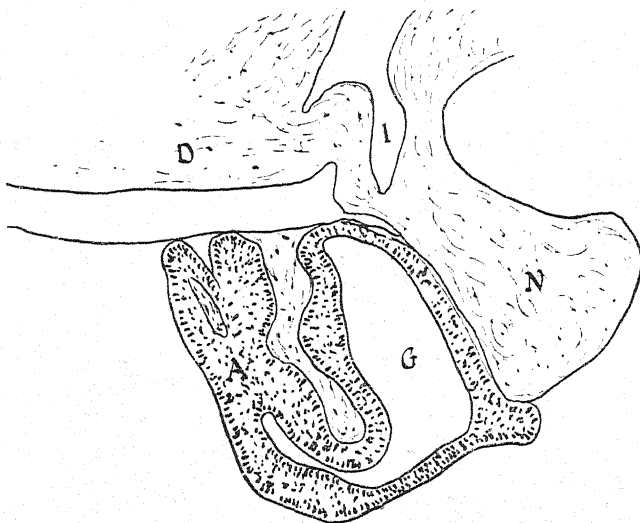


FIG. 12.—Sagittal section 40-mm. embryo. Showing the "anterior lamina" giving origin to the tuberal process which extends almost to the brain-wall. Nasal end to the left.

N, neural lobe; I, infundibulum (cavity of); G, intra-glandular cleft; A, anterior lamina and tuberal process; D, diencephalon.

lying within the intraglandular cleft of the oral lobe, invested on all sides by a thin covering of oral-lobe tissue (Pl. II, fig. 7).

The other striking feature is the presence of a large and well-formed "lobus bifurcatus" or "pars tuberalis" formed as follows: the proximal margin of the oral lobe is bent forwards in its central two-thirds, and passes headwards for some distance rostral to the body of that lobe. This process is lobulated on the surface, and gives off on one side a small lateral branch. It then divides into two horns, right and left, which pass upwards and lie on each side of the infundibular process.

Plate II, fig. 7, shows the arrangement of the parts in transverse section.



## DISCUSSION.

## ORIGIN AND COMPOSITION OF THE ORAL LOBE.

1. *Early Stages.*

The accepted view of the origin of the oral lobe in man is that it arises as a single median depression in the roof of the stomodeum. The single specimen in my own collection which illustrates this stage corroborates this view and bears a close resemblance to a specimen of similar age described by RUDEL. It seems probable, however, from the study of a later stage, that this single rudiment is in reality a composite one. The evidence of comparative embryology indicates the presence of more elements than one in the oral recess. It has been shown by GAUPP that in *Lacerta* the oral lobe has a triple origin, and that it consists of three parts, a central and two lateral, opening separately into the mouth cavity, while later the portion of the mouth cavity into which they open is drawn up into the primitive rudiment, constituting a "Vor-raum." In the chick, ROSSI showed that the oral rudiment is composed of a central and two lateral parts, which open into the mouth cavity by a common canal.

In Chiroptera, WEBER recognised a median and two lateral parts, and showed that the lateral parts are centres for the formation of the glandular part, and that the median part does not take part in the process but atrophies.

The condition in the 6-mm. embryo recorded here is of value in this connection. In it the oral pocket consists of a short central stem, from whose distal end there extend two lateral pockets, indicating that the early rudiment in man, a single median pocket, represents a central and two lateral parts, which become distinct from one another as development proceeds, opening into the mouth cavity by a single orifice. Thus the development of the human hypophysis falls into line with that of reptiles, birds, and chiropters. This condition is, however, temporary, for at the 8-mm. stage the recesses are incorporated into a single chamber showing no differentiation of its parts.

While the separate existence of these parts is lost after a short interval, the distinction remains, in so far as the lateral margins form, as will be shown, the principal source for the formation of the lateral parts, and the central part for that of the central portion of the adult oral lobe.

2. *Later Phases of Development.*(1) *Stalk Formation.*

Tracing the parts played by the various portions, we can recognise, first, the division of the oral pocket into the stalk and the glandular portion proper. All that need be said in regard to this is that, after the 8-mm. stage, there is a definite diminution in the size of the proximal or root portion of the pocket, and a progressive increase in the width of the distal or apical portion.

The change corresponds to the increasing density of the tissues round the root leading up to the formation of the cartilaginous basis cranii. The further changes in the root portion need not be described in detail. They consist in a gradual diminution in the size of this structure, with obliteration of its lumen, and under ordinary circumstances this portion produces no "glandular" tissue such as is found in the fully developed hypophysis.

(2) *Parts forming the Adult Oral Lobe.*

From the stage represented by the 12.5-mm. embryo onwards there occur the developmental changes which lead to the adult form of the gland, and particularly notable are the changes in the oral lobe.

Three portions of the original oral pocket are specially active in this process, and the parts derived from each of these centres appears to retain to a considerable degree its identity in the adult.

These parts are the lateral margins, the proximal border (of the distal portion), and the central part of the rostral surface.

1. *The Lateral Margins.*—These are regions of specially active enlargement, and their growth occurs in such a way that the tip of the lateral margin turns rostrally and medially.

At first the intraglandular cleft is continued forwards to the tip of the growing margin, but the cleft becomes obliterated in front by the adherence of the opposite sides to one another.

These lateral margins are responsible for the formation of the "lateral masses" of the oral lobe.

The curved medial surface of this growing portion is limited by connective tissue, which marks off the portion of the adult gland derived from this source, separating it from a central mass which may now be described.

2. *The Central Part of the Rostral Surface.*—On the centre of this surface in the 12.5-mm. stage there is a prominent ridge, the continuation upwards of the stalk of the gland. In the later stages this is represented by a mass or a nodule, especially distinct on the lower proximal part of this surface (Pl. I, fig. 3, 3 and fig. 5, 5). This nodule becomes of considerable size, and projecting rostrally it comes into contact with the third element which I have termed the anterior lamina. On each side of the central mass thus formed are the lateral masses, but, as has already been mentioned, there is a strand of connective tissue between the two elements. The central mass consists of glandular tissue in part, but with this glandular element there is also a certain amount of fine connective tissue derived from the thin layer which intervenes between the oral and the neural lobes.

3. *The Proximal Border forming the "Anterior Lamina."*—The successive growth changes which occur in this portion are shown in the models, Plate I, figs. 1, 3, 4, and 5.

From these it is seen that from this margin there grows rostrally and towards the floor of the brain, a thin lamina which stretches across from one side to the other, and joins the lateral masses to one another. This lamina becomes thicker, its margin at first is nodular and then papillary, and grows so far as to cover over the whole of the original rostral surface of the gland.

As seen in the 40-mm. embryo, its margin extends as far as to the floor of the brain-wall (fig. 12), rostral to the root of the infundibulum.

In the centre this thin lamina fuses with the free surface of the central mass, and I have not been able to determine any structural differentiation between these two elements.

In embryos of more advanced development, 60 mm. and 90 mm. length, which I have examined, the arrangement of the parts was the same as in those of 30 and 40 mm., but the "anterior lamina" had extended further towards the brain.

As the infundibulum becomes elongated, the extremity of this lamina does not reach the brain, but is applied to the infundibulum only.

This element represents the "pars tuberalis" of other forms, which must be shortly described.

## PRESENCE OF A "PARS TUBERALIS" IN THE HUMAN HYPOPHYSIS.

The term "pars tuberalis" was introduced by TILNEY in 1911 to indicate a portion of the hypophysis which, he claimed, had not been previously described or recognised, and which possessed definite histological and embryological characteristics.

Its distinctive embryological character in, for example, the cat is its formation from bilateral hollow tubercular outgrowths from the rostral surface of the oral lobe, at or near the junction of the proximal or stalk portion with the more distal part.

"It has its origin in two secondary diverticula or sprouts from the body of the pituitary sac.

"These sprouts, the tuberal processes, ultimately fuse with one another across the median plane, displace the body of the pituitary sac ventral, and thus secondarily assume their juxta-neural position." (TILNEY, *Internat. Monatsschrift*, Bd. xxx, 1913, p. 286.)

These sprouts appear at an early stage, while Rathke's pocket is still in free communication with the mouth cavity. In the cat the outgrowth occurs while the oral lobe has very much the form and condition found in the 12.5-mm. embryo figured and described before. The outgrowths occur from the sides of an anterior keel of the triradiate part such as is shown in Plate I, fig. 1.

These outgrowths increase rapidly in size, are directed towards the distal margin of the pocket, fuse with one another, and again bifurcate to enclose the stalk of the neural lobe.

TILNEY gave to it the name "pars tuberalis" from the close relationship which it presents to the tuber cinereum on the floor of the diencephalon.

While to TILNEY must be ascribed the credit for the recognition and description of this element in the pituitary, yet it is clear that other workers prior to him had noted its occurrence in various forms.

In 1905 STADERINI (3) described as a "lobule de la tige" an outgrowth from the hypophysis towards the optic commissure, and the same part was recognised by JORIS in 1908. BOLK (11), in his account of the hypophysis in *Tarsius*, recognised and carefully described as the "lobulus bifurcatus" a portion of the hypophysis which grew upwards and divided to enclose the stalk of the infundibulum. HERRING (6), in 1908, mentioned the presence of a "tongue-shaped process" in the developing hypophysis, which appears to be the same structure as that described by the other writers named.

TILNEY's "pars tuberalis" is clearly the same as the "lobule de la tige" of STADERINI, the "lobulus bifurcatus" of BOLK, and the "tongue-shaped process" of HERRING.

WOERDEMAN's (9) important paper in 1915 deals fully with this part of the gland in many of the vertebrates, and using BOLK's terminology of "lobulus bifurcatus," he shows the variations and significance of this element in different forms.

The "lobus tuberalis" has been identified by other writers, by BAUMGARTNER (5) in fishes, reptiles, and amphibia; by ATWELL (8) in the rabbit, and by Miss PARKER (7) in marsupials.

BOLK has shown that the "lobus tuberalis" is a prominent element in the developing hypophysis of *Tarsius spectrum*. WOERDEMAN figures some specimens of the hypophysis in *Tarsius* embryos, and I have above described and figured another specimen.

In this, as in other specimens of *Tarsius*, the "lobus tuberalis" originates from a single lamina, the "corpus lobus bifurcati," and divides into a fork enclosing the stalk of the neural lobe.

In the human embryo the process which gives rise to this part is somewhat different.

The beginning of a new formation is shown in embryo S. III, Plate I, fig. 3. In this



specimen the distal portion of the pocket has no longer the leaf-shaped form found in the earlier specimen (fig. 1), of which the wide distal part of the pocket narrows gradually to the stalk.

The stalk has become distinct from the glandular part, and the proximal margin of the glandular part has widened out and is turned rostrally.

Pl. II, figs. 4 and 5, show later stages of the process, by which a thin lamina of epithelial tissue is formed, stretching across from one thickened lateral margin to the opposite one, and covering over a thickened central mass on the rostral surface of Rathke's pocket.

The margin of this lamina is lobulated, and it gradually extends distally towards the floor of the neural tube.

In none of the specimens up to 30 mm. does this margin actually reach to or surround the infundibulum. The essential feature, however, of a "pars tuberalis" does not lie in its close apposition to the tuber cinereum, but rather in its developmental and structural characteristics.

The origin of this part is dissimilar from that of a characteristic "pars tuberalis," such as occurs in the cat, in that it does not arise as two separate and distinct buds, but, at the same time, the lamina from which it develops originates from the junction of the stalk with the gland proper. In *Tarsius*, moreover, the root of the "pars tuberalis," as shown in the model, fig. 6 (Pl. II), is a continuous lamina, comparable in its position and form to the lamina found in the human embryo S. III.

I have not been able to determine any histological characteristics which differentiate it in structure from the parts formed from the lateral lobes, but the developmental evidence points clearly to the presence in the human hypophysis of a thin "anterior lamina" which represents the "pars tuberalis" as found in *Tarsius*, but is much smaller.

In none of the human embryos which I have examined have I been able to recognise such "tuberal sprouts" as occur in, for example, the cat.

The only structures which bear a resemblance to such sprouts are the nodules shown on the margin of the "anterior lamina" in Pl. I, fig. 5, from an embryo of 30-mm. length.

This is a stage of development considerably more advanced than that at which in the cat these processes appear, or that at which the "pars tuberalis" appears in *Tarsius*. It seems probable that the thin "anterior lamina" is the part of the human hypophysis which represents the "pars tuberalis" of these forms.

Reference to the model, from a 12.5-mm. embryo, in Plate I, fig. 1, shows that there are no "tuberal sprouts," but at the distal end of the prominence of the stalk there is a projection, rounded and bulging from the rostral surface. This marks the site from which the central part of the thin "anterior lamina," and possibly also that from which the "central mass" arise later.

#### RELATION TO THE STRUCTURE OF THE ADULT ORAL LOBE OF THESE DEVELOPMENTAL ELEMENTS.

Transverse section of the adult hypophysis shows the arrangement of the central and the lateral masses, and the connective tissue in relation to them (Pls. II and III, figs. 8 and 9), which corresponds to the embryological account given above.

In the oral lobe there is on each side a central core of connective tissue, containing blood-vessels, and from each core there can be traced a thin layer of connective tissue spreading back towards the connective tissue in the middle line between the neural and the oral lobes.

There are thus marked out in the oral lobe three areas, a central and a lateral on each

side. In many specimens there can be detected a slight difference in the staining reactions of the central and the lateral parts, the lateral parts being more eosinophile and the central more basophile. The section (Pl. III, fig. 9) shows also in the human hypophysis the absence of the intraglandular cleft, and, as a result, the absence of a distinctive "pars intermedia" such as is present in the majority of the lower mammals.

The neural lobe, which as a rule shows no central canal, but which may contain spaces of some size filled with "colloid" material, is at each side separated from the oral lobe by a thin layer of connective tissue, in which there are small spaces, lined by epithelium. The adjacent layer of the oral lobe stains more deeply with hæmatoxylin than does the rest, and also contains small spaces containing a homogeneous material which with hæmatoxylin and eosin is of a bluish colour. Near the middle line the connective tissue is thicker, and contains many spaces filled with "colloid."

In conclusion, the adult epithelial lobe of the hypophysis comprises, embryologically, the following elements:—

(1) Lateral portion formed by the curving forwards and medially of the lateral margins of Rathke's pocket. The cavity of Rathke's pocket disappears early from these masses. The bending round of the lateral margins enclosed a core of connective tissue, and through the union of the lateral with the thickened lower margin the connection of this core with the exterior is limited to the distal surface of the gland (upper surface of the human adult).

(2) A central portion of variable size, derived from a thickening of the epithelium of the central portion of the anterior wall of Rathke's pouch. This portion intervenes between the two lateral parts.

(3) There is, in addition, on the anterior surface and connected to (2), a thin lamina derived from the lower margin of the gland which grows upwards and connects together the lateral lobes in front of the central nodule.

This part probably corresponds to the "pars tuberalis," but is much smaller than in those other forms in which it has been recognised. It does not as a rule in man extend as far as to the infundibular stalk of the neural lobe.

(4) The intraglandular cleft disappears by fusion of the opposite walls, and the rostral surface of the neural lobe is not, as in other forms, invested by a special layer of epithelium, the "pars intermedia."

The section of the adult gland in Plate III, fig. 9, shows that in the site of the intraglandular cleft and "pars intermedia" there are numerous follicles lined with low columnar epithelium, filled with "colloid" material, which stains with eosin.

There are also smaller follicles, lined with epithelium, which contain a granular material which takes the hæmatoxylin stain.

#### THE NEURAL LOBE.

Up to embryos of the 6-mm. stage there is no evidence of the formation of a "neural" lobe of the hypophysis, and the first indication of its development appears at the 8-mm. stage.

The neural lobe of the hypophysis occurs in all vertebrates with the exception of the elasmobranch fishes in whom, as was pointed out by GENTES, there is no infundibular lobe.

HERRING has pointed out, however, the presence in them of an infundibular canal, into which there opens on each side the orifice of the "saccus vasculosus."

He has further shown that the saccus vasculosus arises in them "comparatively early by the outgrowth of the wall of the cerebral vesicle on either side."

In man, the formation of the neural lobe is usually ascribed to a simple evagination of the floor of the diencephalon.

Examination of the earlier specimens here described shows, however, that the development is not so simple.

The evidence which they afford is consistent, and shows that, in man, the origin of the neural lobe involves a long area of the floor of the diencephalon, extending backwards for a considerable distance from behind the region of the chiasma. In this area there is a central thickening and rapid growth of the floor of the diencephalon, producing a thickened ridge whose inner convex surface projects into the lumen of the neural tube.

On each side of the central ridge is a slit-like recess, which is more than merely the marginal depression by the side of the ridge, but forms on each side a distinct evagination towards the exterior.

The external central projection which marks the neural lobe lies in the main caudal to the lateral pockets. The condition here described is particularly evident in the sections of the 8-mm. embryo, which are cut transversely, and in the 12.5-mm. specimen. It is not readily recognised when the sections are in the sagittal plane.

In the 12.5-mm. embryo there is a long central ridge in the floor of the diencephalon, with lateral slit-like pockets.

As the infundibular projection increases, the lateral pockets become less distinct.

In searching for an explanation of this condition, it occurred to me that the lateral recesses may have some relation to the "saccus vasculosus" found in selachian fishes as well as in other forms.

The resemblance is not identical, for the "sacci vasculosi" are stated to be lateral prolongations of the median "saccus infundibuli," and open by a median orifice on the dorsal wall of the infundibular lobe. HERRING states that in selachians the "saccus vasculosus" appears as an outgrowth of the cerebral wall on each side (of the infundibulum).

In the 8-mm. embryo described (fig. 6), if this view be correct, the central recess is the true "infundibular funnel," and the lateral pockets on either side of it are recesses representing the lateral "saccus vasculosus" outgrowths of the selachians.

In the 12.5-mm. embryo the triple recesses are very clear, central, and lateral, but the lateral recesses are relatively small, and do not form a projection on the exterior.

CHIARUGI (13) has identified a portion of the posterior floor of the diencephalon and of the process of the infundibulum, possessing a nodular outline, as representing in mammals a rudiment of the "saccus vasculosus," but he has not shown the grooves and the folding of the floor in this region which are demonstrated in this paper in the human embryo.

The tissue forming the infundibular lobe is continuous with the ependymal layer of the neural wall, and resembles it in its staining reactions.

At first this lobe is hollow to its end, but the cavity is irregular in outline and commonly is obliterated in the older specimens. The Tarsius embryo shows complete obliteration of the central lumen where the infundibular region is enclosed by the oral lobe. As the infundibular lobe grows out, it comes to lie on the distal margin of Rathke's pocket, and passes on to the caudal wall of that cavity.

The lateral margins of the distal border increase and invest the sides of the neck of the infundibulum.

These appear, in man, to be the source of the glandular tissue found frequently around the stalk of the adult neural lobe. In other forms, this investing layer is derived from the



upgrowing "pars tuberalis" (WOERDEMAN). In *Tarsius*, the neural lobe invaginates the caudal wall of the oral lobe, and is completely invested by it.

This condition does not occur in man.

#### SUMMARY AND CONCLUSIONS.

Study of the development of the human hypophysis brings out the following conclusions :

- (1) The oral lobe appears as a single median depression in the root of the stomodeum. This single depression, however, alters in shape and forms a central stem with two lateral horns, which probably represent the central and lateral chambers described in reptiles. This stage is transitory.
- (2) The proximal portion of the oral outgrowth is transformed into the stalk, while the distal portion above gives rise to the epithelium of the oral lobe of the hypophysis. Three parts can be recognised in this, a lateral on each side, a central, and a thin anterior lamina, and their origin is as follows :—
  - (a) The lateral margins of the oral pocket form the lateral parts.
  - (b) The central part of the rostral surface forms a cone or plate of tissue intervening between the lateral lobes.
  - (c) From the proximal margin an outgrowth takes place which forms a "pars tuberalis," ultimately represented by a thin lamina on the rostral surface of (b) uniting the lateral lobes.
- (3) The caudal wall of the oral lobe for a time invests the adjacent surface of the neural lobe and forms a "pars intermedia," separated by the intraglandular cleft from the anterior lobe proper.
- (4) The intraglandular cleft disappears at an early stage on each side in the "lateral parts," by fusion of the opposite surfaces, and later on disappears almost completely centrally.
- (5) There is in the adult human hypophysis no definite "pars intermedia" and no distinct intraglandular cleft.

The oral and neural lobes are separated by a thin connective tissue, in whose central part are numerous follicles containing colloid or a granular material.
- (6) The neural lobe represents, not only a median unpaired outgrowth, but also contains the rudiments which represent the bilateral "saccus vasculosus" of elasmobranch fishes.

I have to express my thanks to Professor BRYCE of Glasgow University for the opportunity of examining and reconstructing the hypophysis in a 30-mm. embryo, and of examining sections of embryos of 40, 50, and 90 mm. length of his collection ; to Dr R. J. GLADSTONE for similar use of his sections of a 10-mm. embryo ; to Professor BOLK of Amsterdam for the invaluable privilege of examining his large collection of sections illustrating the comparative embryology of the hypophysis, especially its development in *Talpa* ; to Dr ARIENS KAPPERS for similar privileges of examining material in his Laboratory ; and to Dr DE LANGE for the use of suitable material from the Hubrecht Embryological collection in Utrecht.

Part of the expenses of the preparation of this paper have been borne by the Harvey Hadden Research Fund in Anatomy and by the Anstruther of Charleton Memorial Fund of the University of St Andrews.

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EXPLANATION OF PLATE FIGURES.

PLATE I.

Fig. 1. Wax plate model of hypophysis of 12.5-mm. human embryo. Magnification of model, 100 diameters. Rostral view of the oral lobe.

Fig. 2. Transverse section of oral and neural elements from the same embryo as fig. 1.

1. Central internal ridge in floor of diencephalon.
2. Infundibular process
3. Lateral neural recess.
4. Cavity of infundibulum.
5. Cavity of oral lobe (intraglandular cleft).

Fig. 3. Wax plate model of hypophysis of 20-mm. human embryo. Magnification of model, 50 diameters. Rostral view of the model, showing the infundibular recess in the floor of the third ventricle.

1. Orifice of the infundibulum.
2. Lateral margin; 3. central mass; and 4. thickened proximal margin, which later forms the "anterior lamina" of the oral lobe.

Fig. 4. View similar to fig. 3 of wax plate model of hypophysis of 26-mm. human embryo.  $\times 50$ . Parts as in fig. 3. The central mass is covered by the anterior lamina.

1. Orifice of the infundibulum in the floor of the third ventricle.
2. Thickened lateral margins, turned towards rostral surface, and continued into the bent proximal margin. This has turned distally, and covers the "central mass" at 3.

Fig. 5. Similar view of a wax plate model of the hypophysis of a 30-mm. human embryo, oral lobe only.  $\times 50$ .

1. Recess on distal border for the neural lobe.
2. Lateral mass.
3. Anterior thin lamina.
4. Central mass from rostral surface.
5. Nodular projection of margin of the anterior lamina.

PLATE II.

Fig. 6. Similar view of a wax plate model of the hypophysis of a *Tarsius* embryo.  $\times 66$  diameters.

1. Infundibulum.
2. Lateral mass.
3. Tuberal process.
4. Anterior lamina.

Fig. 7. Transverse section of the hypophysis in a *Tarsius* embryo, showing the neural lobe completely invaginated into the interior of the cavity of the oral lobe. The section shows also the pars tuberalis, P.T.1, and an offshoot from it, P.T.2. P.L., lateral mass. P.N., neural lobe. P.I., layer of oral lobe investing the neural lobe. L, intraglandular cavity of the oral lobe. Magnification,  $\times 125$ .

Fig. 8. Transverse section of the pituitary fossa and of the human adult hypophysis *in situ*, to show the lateral cores of connective tissue, the central mass between them, and the lateral masses on each side, also the absence of an intraglandular cleft and of "pars intermedia." Rostral (anterior of adult) surface above.

- A, cavity of sphenoidal sinus.
- B, connective-tissue investment.
- C, central mass of the oral lobe.
- D, core of connective tissue.
- E, lateral mass of oral lobe.
- F, nodules of colloid.
- G, neural lobe.
- H, lymph space in the periglandular connective tissue.
- K, dorsum sellae of the sella turcica.

## PLATE III.

Fig. 9. Central portion of a transverse section of a human adult hypophysis, showing the central and lateral parts of the oral lobe, the absence of the intraglandular cleft and "pars intermedia," and the neural lobe.

- A, central mass.
- B, core of connective tissue, between central and lateral masses.
- C, lateral mass.
- D, neural lobe.
- E, thin connective tissue, &c., between the two lobes.

## ADDENDUM.

In a paper which was published while the foregoing paper was being completed, ATWELL (*American Journ. of Anat.*, vol. xxxvii) describes and figures a series of human embryonic hypophyses. Dealing with the origin of the "pars tuberalis," he figures a reconstruction from an embryo of 14-mm. length, which in its general form closely resembles that from a 12.5-mm. embryo figured here.

On each side of the lateral margin at the root of the stalk he describes a small nodular projection, which he considers to be the rudiment of the "pars tuberalis," and shows its presence also in embryos of 16 and 17 mm. length. He terms it a "thin epithelial shelf."

The 12.5-mm. embryo reconstruction figured here does not show a definitely recognisable separate nodule such as is present in his specimens.

The "thin epithelial shelf" of his specimens appears to be the same as what I have here described as the "thin anterior lamina," springing from the lower border of the proximal portion of the glandular part of the oral pocket.

Other questions dealt with in this paper are not mentioned by ATWELL.





Dr DAVID WATERSTON : "The Development of the Hypophysis Cerebri in Man."—PLATE I.

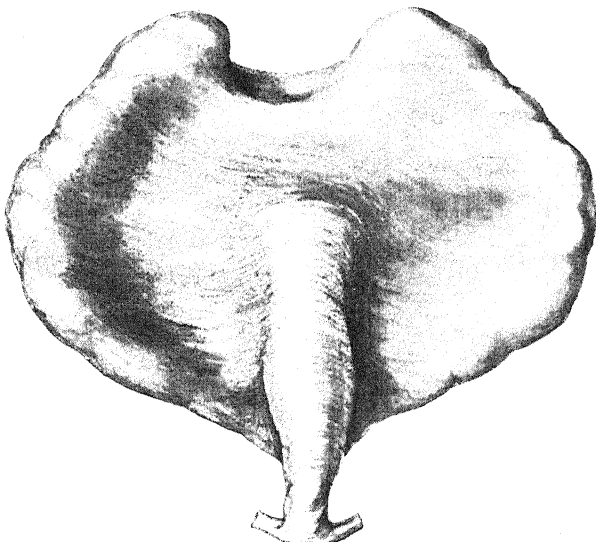


FIG. 1.

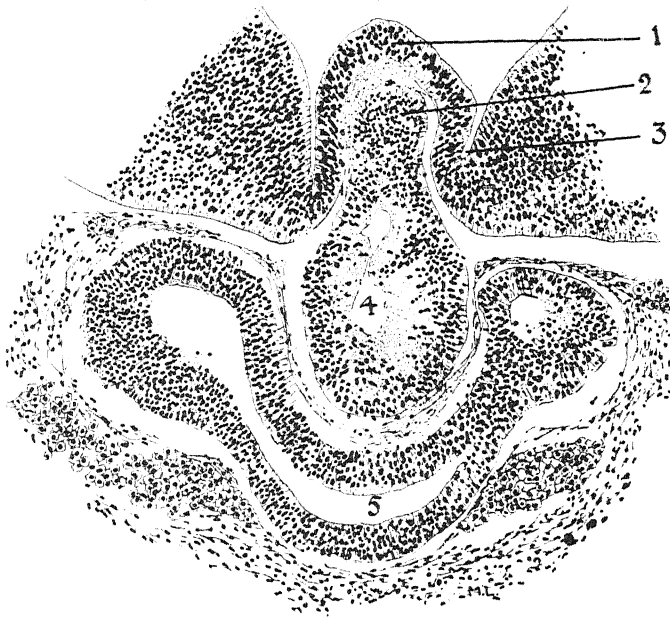


FIG. 2.

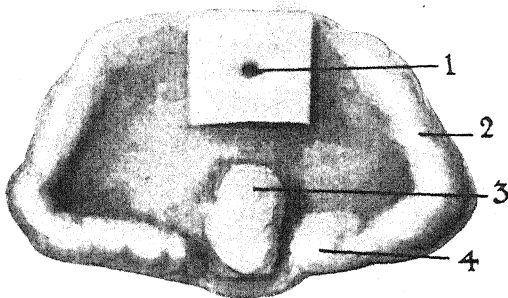


FIG. 3.

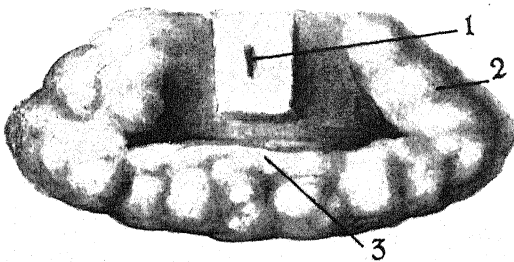


FIG. 4.

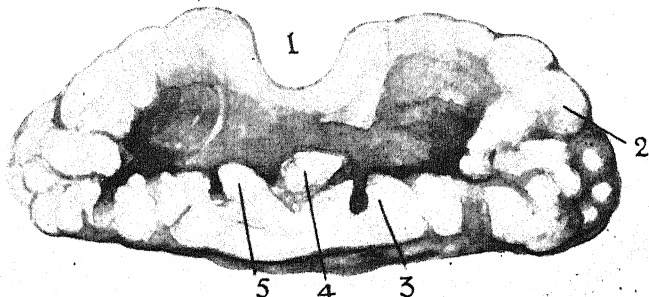


FIG. 5.





Dr DAVID WATERSTON : "The Development of the Hypophysis Cerebri in Man."—PLATE II.

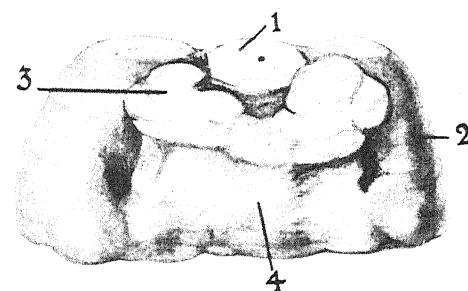


FIG. 6.

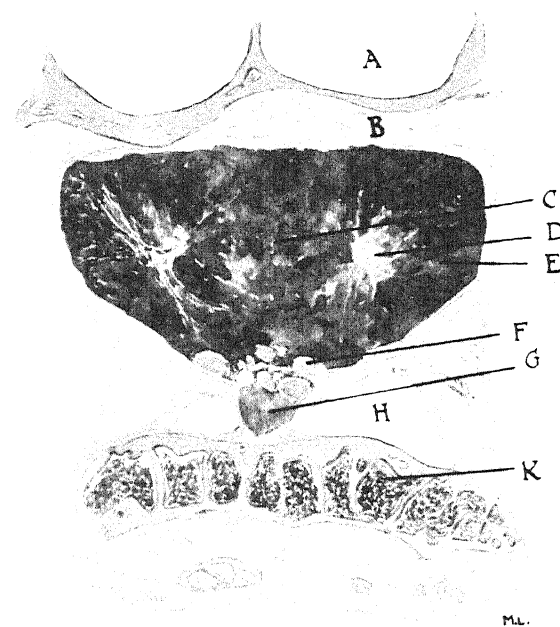


FIG. 8.

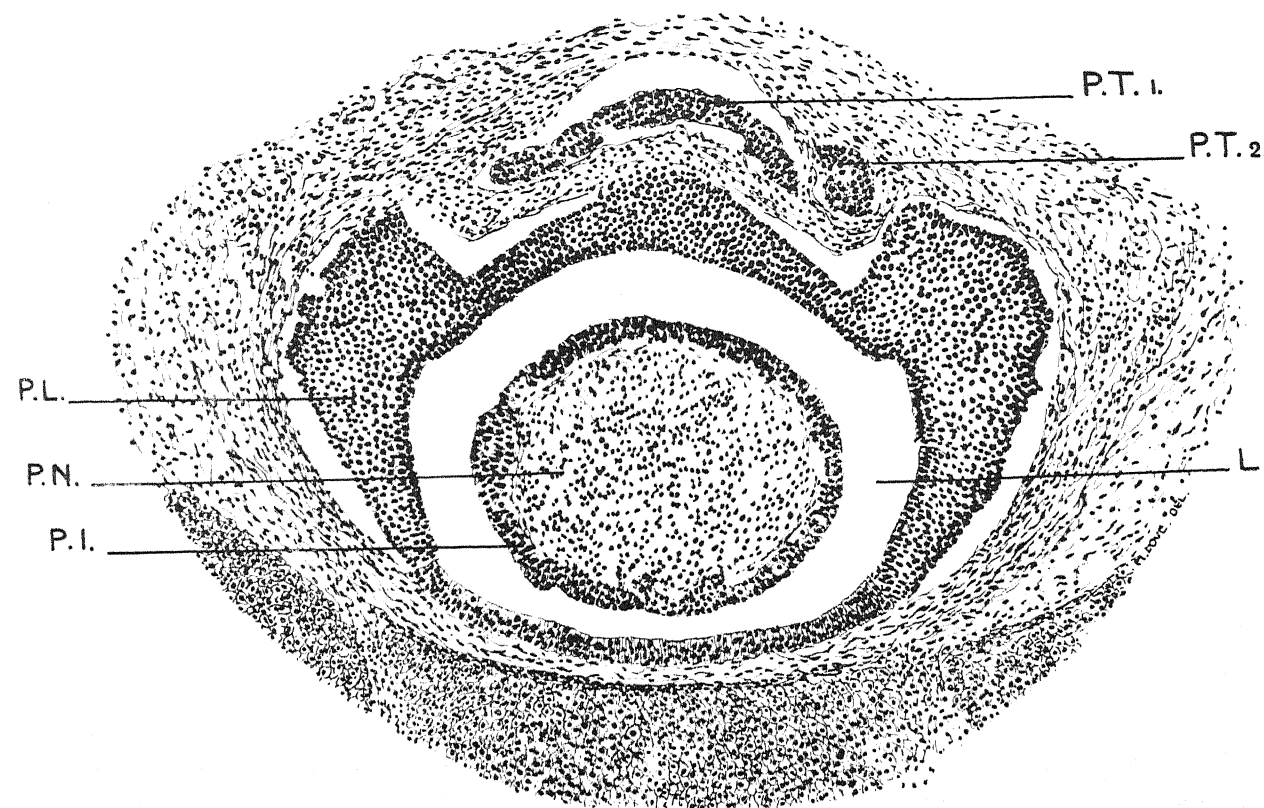


FIG. 7.



Dr DAVID WATERSTON: "The Development of the Hypophysis Cerebri in Man."—PLATE III.

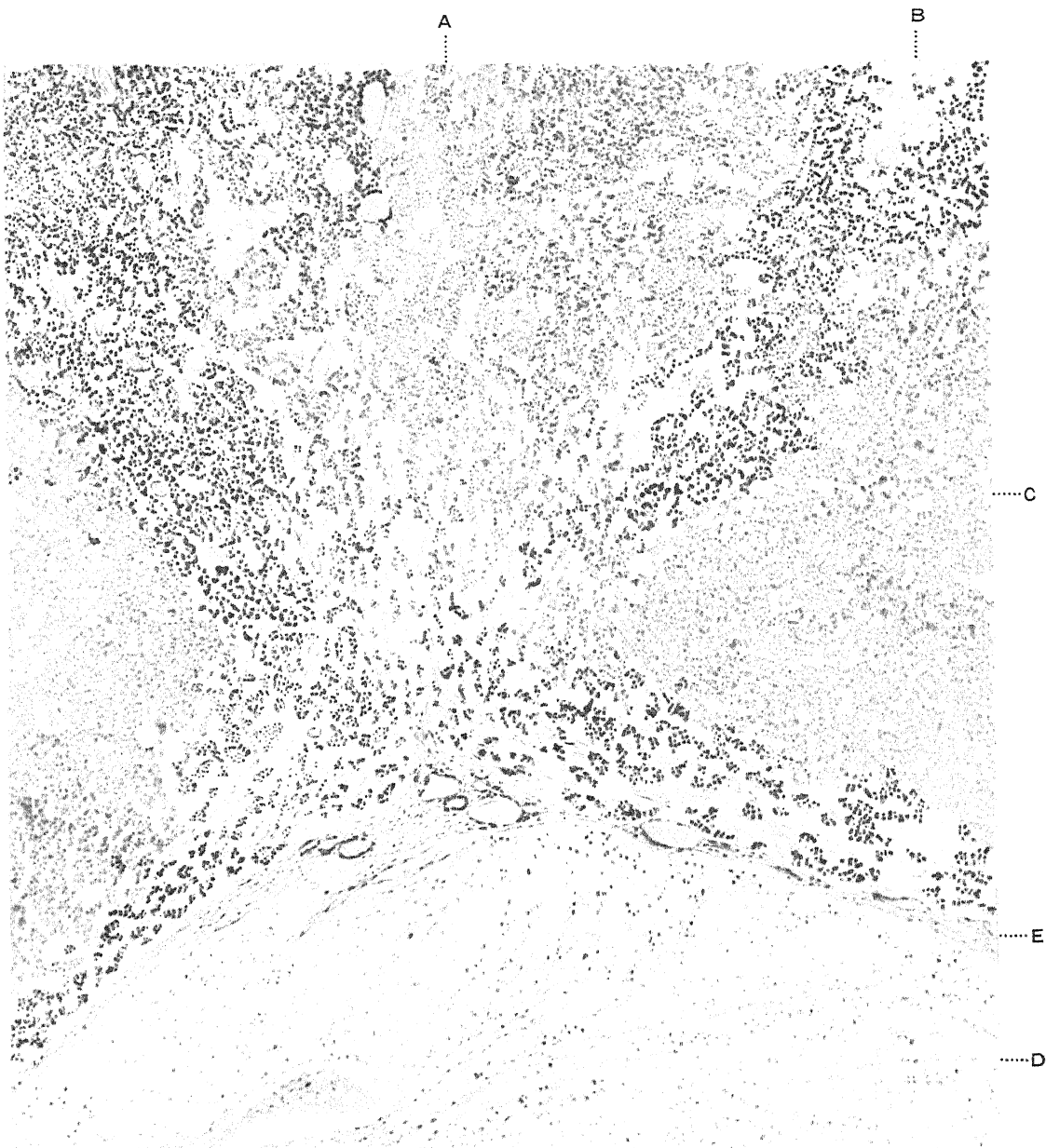


FIG. 9.





VII.—The Igneous Geology of Ardsheal Hill, Argyllshire. By Frederick Walker, Carnegie Teaching Fellow, St Andrews University. (With One Plate and Two Text-figures.)

(MS. received October 23, 1926. Read December 6, 1926. Issued separately February 21, 1927.)

Ardsheal Hill is situated in Argyllshire amidst country of great petrographic interest. It is easily reached by road or rail, for it overlooks the main road from Oban to Fort William, and is under 2 miles from the station of Kentallen on the Ballachulish Branch of the L.M.S. Railway. The area considered in the present communication is bounded by Loch Linnhe on the west and on the east by the above-mentioned road.

Ardsheal Hill summit, which is the culminating point, reaches a height of 863 feet. The higher slopes of this hill are mainly peaty moorland, but farther down they are tree-clad, particularly to the north-west. Exposures occur for the most part on rocky knolls, or in stream-sections, while one intrusion has been laid bare by wave-action on the shore.

The igneous rocks of the area range from subacid to ultrabasic, showing great diversity of types, especially in the small complex which forms the summit of the hill. All these types may be referred with some probability to the Lower Devonian igneous activity which was so pronounced in the surrounding district.

A list of the rock types recorded on Ardsheal Hill is appended below:

Granodiorite.	Augite-diorite.
Granophyre.	Appinite.
Quartz-porphyrityte.	Kentallenite.
Hornblende-porphyrityte.	Olivine-basalt.
Plagiophyre.	Hornblendite.
Camptonite.	

All these types are represented in the summit complex, with the exception of the first and third.

#### PREVIOUS INVESTIGATION.

Ardsheal Hill itself has received but scant attention from petrologists, although many neighbouring areas have had their igneous geology described in great detail. The type occurrence of kentallenite, for instance, is only a mile to the north-east. The late Mr J. S. GRANT WILSON was the first to note the presence of augite-diorites on Ardsheal Hill,\* while some years later Mr E. B. BAILEY, writing on the augite-diorites of the district, mentions that "The more dioritic facies with only very subordinate orthoclase are represented by a specimen from Ardsheal Hill."† He also records the presence of "a small quantity of interstitial quartz and alkali felspar in the augite-diorites of Rudha Mor and Ardsheal Hill."‡ In the earlier instance the view is taken that these augite-diorites are merely "basic modifications of the magma which has produced the larger granite-masses of Ballachulish and Ben Nevis." These diorites are said by Messrs HILL and KYNASTON to resemble strongly the

\* *Ann. Rep. Geol. Survey*, 1896, pp. 21-2.

† *Mem. Geol. Survey*, Sheet 53, 1916, p. 170.

‡ *Op. cit.*, p. 155.

augite-diorites of Glen Strae.\* Sir JOHN FLETT has also commented on the affinities of the Ardsheal diorites with certain masses associated with the Cruachan granite.†

Some years ago the present writer noted the great diversity of rock-types on Ardsheal Hill, and an investigation was undertaken later in collaboration with Mr A. M. COCKBURN, during which the area was re-mapped, many interesting points being discovered. The results of this preliminary investigation were embodied in a short paper which is published in abstract in the *Transactions of the Edinburgh Geological Society*. The investigation was recently completed by the author, and the results are made available in the present communication.

The igneous rocks of the Ardsheal area are all intrusive and, with the exception of a few dyke-like occurrences of porphyrite, are plutonic, having the form of small bosses. They are intruded into the following metamorphic series:—

Cuil Bay Slates.  
Appin Phyllites.  
Appin Limestone.  
Appin Quartzite.

Except in the case of the augite-diorite intrusion of Rudha Mor, these metamorphic strata are affected at their junctions with the Ardsheal intrusions by the metamorphic aureole of the Ballachulish "granite." The contact metamorphism round this large intrusion has greatly obscured that caused by the smaller igneous masses of Ardsheal. The metamorphic aureole of the Ballachulish "granite" has been fully

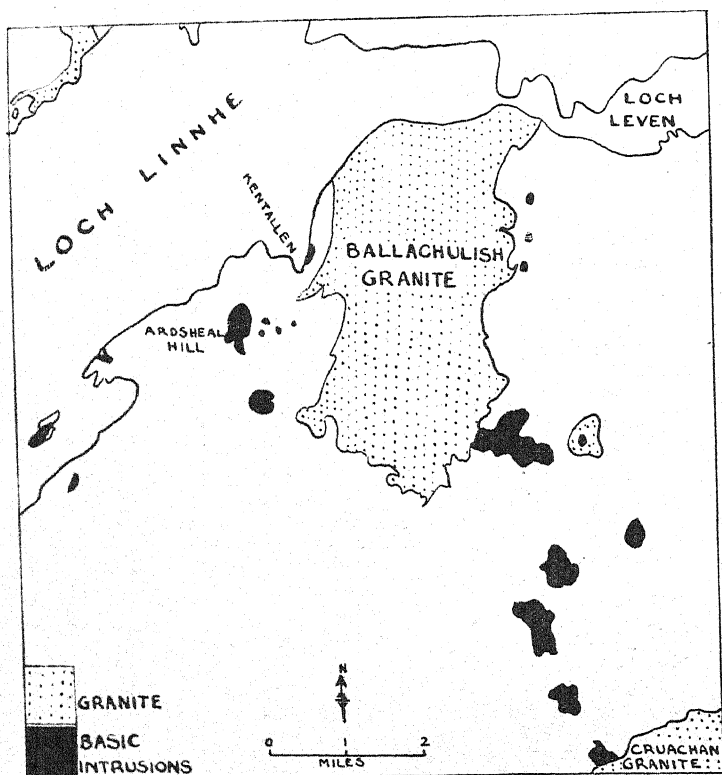


FIG. 1.—Sketch Map showing basic intrusions round Ballachulish Granite.

described with other neighbouring ones by Mr E. B. BAILEY.‡

#### SUMMIT COMPLEX.

The most important intrusion to be dealt with is the complex forming the summit of Ardsheal Hill. It covers quite a small area measuring 600 yards N.S. by 300 yards E.W.,§ and stands out prominently from a boggy plateau just below the 800-foot contour. In spite of its small size, however, it contains no fewer than nine rock-types.

#### PETROGRAPHY OF SUMMIT COMPLEX.

The bulk of the summit complex is made up of a rock consisting essentially of augite, olivine, and plagioclase, with variable amounts of orthoclase and biotite. This type shows

\* *Q.J.G.S.*, 1900, p. 547.

† *Mem. Geol. Survey*, Sheet 53, pp. 187-201.

‡ *Mem. Geol. Survey, Dalmanly District*, 1908, p. 91.

§ The area allotted to this intrusion on the Geological Survey maps appears to err on the generous side. See large scale map, p. 150.



many textural modifications which appear to be intimately related. The most striking of these is undoubtedly a black olivine-basalt occurring chiefly in the low cliffs S.E. of the summit. Augite in large phenocrysts and smaller grains of green olivine are the only constituents visible in the hand-specimen. Under the microscope the large augites are equally prominent, but are seen to be composite for the most part; lamellar twinning is also common. This pyroxene is of a pale green colour, showing well-marked zonary banding, especially under crossed nicols, and has a maximum extinction angle of  $43^{\circ}$ . Individual crystals are usually idiomorphic and extremely variable in size, the mineral making up about 15 per cent. of the rock. Well-formed crystals of olivine are also conspicuous, and while likewise variable in size are seldom composite. Black reaction rims of magnetite render them particularly prominent, while the interior of the crystals is frequently crowded with minute rod-like inclusions of magnetite, giving the mineral a brownish-grey colour as in the kentallenites. Olivine does not amount to more than 8 per cent. of the rock. The groundmass is composed of felspar and tiny crystals of magnetite. The bulk of the felspar is an acid labradorite occurring in small laths of variable size, but there is a good deal of cloudy interstitial orthoclase present. The rock was analysed by Mr W. H. HERDSMAN, and the result shows clearly its strong affinity to an orthoclase-olivine-basalt from Taynuilt analysed by Mr E. G. RADLEY.

In places the rock becomes considerably coarser, biotite making its appearance. This mica is markedly poekilitic even in the hand-specimen, and a similar relationship between augite and olivine comes into evidence. The rock may then be classed as a porphyritic kentallenite, having, indeed, a very strong resemblance to the kentallenites of Balnahard\* and Glen Orchy.† All gradations from porphyritic kentallenite to orthoclase-olivine-basalt may be seen, the augite retaining its well-marked porphyritic character throughout; but the kentallenite is confined to the southern half of the complex. The olivine is usually quite fresh in the basalt, but in the coarser modifications it is more often weathered to magnetite (generally marginal), carbonates, and chloritic substances. The augite and plagioclase are in good preservation, but the orthoclase is nearly always cloudy. Close to the actual summit a rock is seen which, although it shows a resemblance to the porphyritic kentallenite, is much more decomposed and poorer in olivine and orthoclase. Epidote and carbonates are conspicuous decomposition products in this rock, which is probably to be correlated with the augite-diorite referred to by Mr BAILEY.‡

To the north and west of the hill hornblende makes its appearance prominently, the rocks in this portion being for the most part appinites. Schlieren with modifications of widely differing texture are conspicuous, while the relative proportions of felsic and mafic minerals are also extremely variable. Some modifications are quite light in colour, containing only 20 per cent. mafic minerals, but others are made up almost entirely of hornblende, being in fact typical hornblendites like those of Colonsay.§ The hornblende crystals are here very large, measuring up to an inch in length. A typical appinite containing between 60–70 per cent. amphibole is seen under the microscope to consist essentially of stout idiomorphic needles of greenish-brown hornblende, with pleochroism X olive-green, Y yellowish-brown, Z greenish-brown, and a maximum extinction angle of  $20^{\circ}$ . This amphibole appears to decompose to a greenish variety and frequently contains small sharply-defined cores of colourless pyroxene. Twinning is common in the hornblende. The only other ferro-magnesian constituent present is biotite, which forms 1–5 per cent. of the rock and is usually enclosed by amphibole. A few small crystals of sphene may occasionally be observed. The felsic

\* *Mem. Geol. Survey, Colonsay*, 1911, pl. vi.

† *Loc. cit.*

‡ HILL and KYNASTON, *Q.J.G.S.*, 1900, pl. xxv, 2.

§ *Mem. Geol. Survey, Colonsay*, 1911, p. 29.

minerals, which occur interstitially, consist of strongly zonal tables of basic plagioclase (mainly andesine-labradorite) which are idiomorphic towards a subordinate amount of orthoclase and quartz. These last minerals are usually in micrographic intergrowth. Magnetite, pyrite, and apatite are sparse accessories, together making up about 1 per cent. of the rock.

In the more acid modifications the felsic minerals are much decomposed, but have apparently similar composition, the same being true in the more basic varieties which grade into hornblendite. A chemical analysis of a basic appinite with about 80 per cent. mafic minerals has been made by Mr W. H. HERDSMAN, and is discussed below. The above hornblendic rocks show many points of similarity to the diorites and hornblendites of Garabal Hill.\*

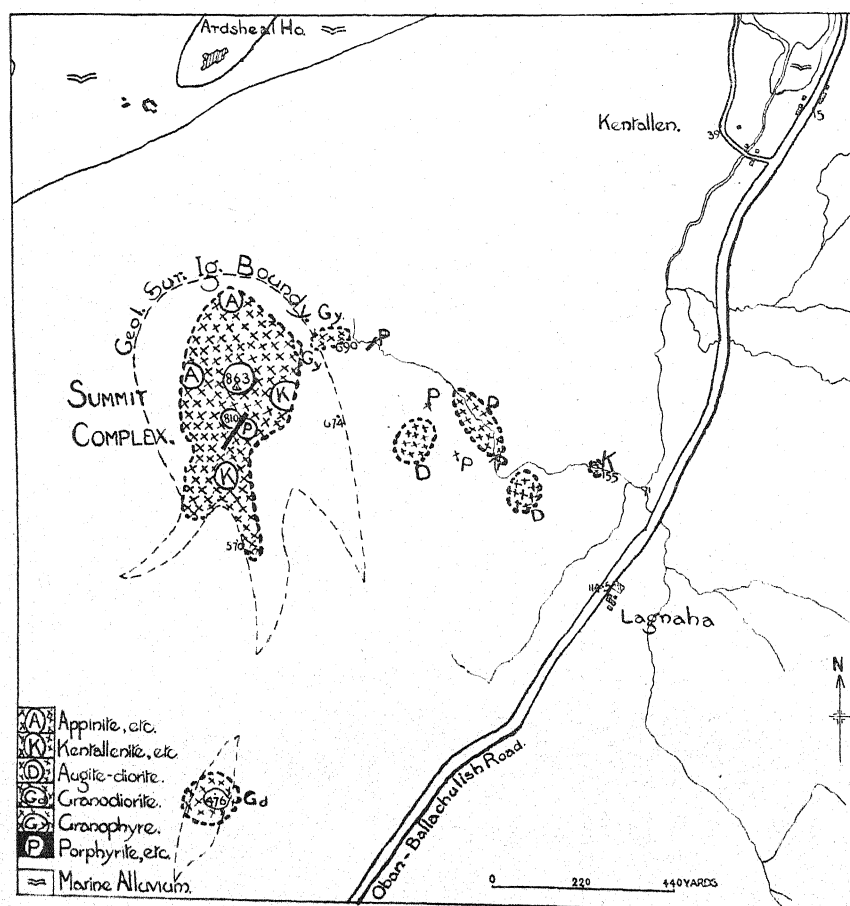


FIG. 2.—Map showing intrusions near summit of Ardsheal Hill. Letters on Summit Complex indicate dominant rock-types at various points.

In the southern portion of the complex another type of appinite is encountered and may be seen in contact with the surrounding schists against which it shows an almost unchilled junction. This rock is composed essentially of large needles of brown hornblende, without any tinge of green, embedded in a finer matrix of plagioclase felspar and micropegmatite. The amphibole is frequently twinned, has a maximum extinction angle of  $17^\circ$ , and forms 20–25 per cent. of the rock. The groundmass is largely decomposed, but the plagioclase, which is much more abundant than the micropegmatite, appears to be labradorite. Green epidote is very common, sometimes occurring as aggregates of radiating needles, while magnetite or ilmenite is an abundant accessory. In places this rock forms curious hybrids with the basalt-kentrallenite magma, which will be considered later.

\* WYLIE and SCOTT, *Geol. Mag.*, 1913, pp. 536–7.

About 75 yards S.W. of the summit a dyke-like mass some 3 feet broad is exposed for a small distance and is seen to be intrusive into both appinite and orthoclase-basalt. When the thin, light-coloured crust is broken off, the dyke rock is seen to be almost black in colour. It is fine-grained, but contains conspicuous phenocrysts of hornblende. Under the microscope this amphibole is found to agree in all its properties with the brown hornblende of the second type of appinite described above. Although such a conspicuous constituent, it does not form more than 7 per cent. of the whole rock. Plagioclase felspar occurs porphyritically in equal abundance, but is too much decomposed for determination, although in the freshest sections it appears to be andesine. Phenocrysts of partially chloritised biotite are of sparse occurrence and are sometimes completely absent. The groundmass, if considered separately, shows a marked resemblance to rocks described by Dr G. W. TYRRELL \* and Mr J. W. HARRIS † as plagiophyre, and by Mr J. W. LUNN ‡ as malchite. It is formed of small laths of plagioclase felspar (mainly andesine) with quite subordinate quartz and partly chloritised biotite. The rock may be classed as a hornblende-porphyrityte, but in some sections both hornblende and porphyritic plagioclase are entirely absent, giving us plagiophyre or malchite. Both these names have disadvantages. The name "plagiophyre," like "orthophyre," should imply marked porphyritic texture, while "malchite" should indicate microdioritic texture. The rock in question fulfils neither of these conditions, but the terms "orthophyre" and, more recently, "plagiophyre" have been so often employed for non-porphyritic rocks that the abuse has come to be tolerated. The former name, *i.e.* plagiophyre has therefore been chosen for the Ardsheal rock, with the hope that some better way out of the difficulty may soon be found. Sometimes, however, hornblende, instead of failing altogether, occurs locally in sufficient abundance to warrant the inclusion of these basic patches among the lamprophyres. Here, again, a difficulty of nomenclature is encountered. Camptonite at once presents itself as the name for such a type, but this term is best retained for rocks with alkaline affinities, the colour of the amphibole often being taken as a criterion.§ The brown hornblende of the Ardsheal occurrence is quite different in colour from the greenish-brown amphibole of most Lower Devonian lamprophyres, and the name "camptonite" is accordingly applied to the rock in spite of the somewhat calcic nature of the groundmass. The normal porphyrite facies of this dyke-like intrusion has been analysed by Mr W. H. HERDSMAN.

To the N.E. of Ardsheal summit, where the complex emerges from the peaty plateau, there is a small but well-marked offshoot from the main mass. This prominence is made up of a medium-grained, non-porphyritic rock of a pinkish-grey colour with much green chlorite. Under the microscope the rock is seen to be composed essentially of large well-formed crystals of acid plagioclase. These make up about 75 per cent. of the rock and are embedded in a matrix composed mainly of micropegmatite. The former presence of hornblende and biotite is indicated by large pseudomorphs in chlorite: occasionally, however, biotite occurs fresh in large hexagonal plates. Magnetite is a frequent accessory, while secondary calcite is abundant. The relationship of the plagioclase to the micropegmatite, their relative proportions, and the texture of the whole rock are all reminiscent of the Bowden Hill type of quartz-dolerite. The rock is termed granophyre, but it is, unfortunately, much too decomposed for chemical analysis. Farther down the hill to the N.E. there is another small mass of granophyre which may be a continuation of the offshoot described above.

\* *Trans. Glasgow Geol. Soc.*, vol. xv, pt. i, p. 77.

† *Geol. Mag.*, 1926, p. 95.

‡ *Trans. Edin. Geol. Soc.*, 1925, pp. 383-85.

§ *Mem. Geol. Survey*, Sheet 53, 1916, p. 157.



## MUTUAL RELATIONSHIP OF THE VARIOUS TYPES.

It will be seen from what has been written that we have a great many rock-types occurring within an area of  $\frac{1}{10}$  square mile. To determine adequately the mutual relationship of all these types, one would require unusually perfect exposures. Those on Ardsheal Hill are only moderately good, and much uncertainty arises in consequence. There is, however, little doubt that the kentallenite and appinite groups with their various modifications are the oldest in the summit complex as well as the most abundant. The two types are intimately associated, frequently forming contiguous schlieren, the same being the case with the textural and mineralogical variations of each type. These schlieren show sharp junctions which are usually unchilled, although occasionally there is slight chilling of the hornblendic varieties against the pyroxenic.

There are, however, two types of appinite in the summit complex. The type with green hornblende has been already considered, but that with brown hornblende must be treated separately. This type occurs sparingly in the southern portion of the complex alone and is very frequently commingled with the augitic types. Thus in a single section we may have as ferro-magnesian, in one part large, abundant crystals of augite without hornblende, and in another equally abundant brown hornblende without pyroxene. The granophyric matrix of the appinite has wormed its way between the augite crystals and has apparently given rise to amphibole in places by reaction with the pyroxene. The impression gained by examination of these hybrids is that the hornblendic magma penetrated into the augitic while the latter was still hot. There cannot, therefore, be much difference in age between the two types of appinite if this is the case, the evidence making both slightly later than the kentallenite magma. The matrix of the appinite with brown hornblende is more alkaline than that of the appinite with green, a circumstance which may possibly have some connection with the differences of colour in the two amphiboles.

The banding of the varieties containing green hornblende is very striking, the changes in composition and grain being exceedingly abrupt, especially at the extreme north of the complex. At this point the variety of type and texture is comparable with that in some of the teschenitic sills of the Midland Valley of Scotland (*e.g.* Inchcolm \* and Barshaw Park †), or with the banded gabbros of Skye. It is probable that here also the structure is due to "fluxion in a magma which was heterogenous at the time of its intrusion." There can be little doubt that both main types originated from the same magma-basin, and the change from a pyroxenic to a hornblendic facies may possibly be attributed to the migration of aqueous or other fluxes produced, during crystallisation, in increasing concentration in the liquid portion of the magma. In the appinites the large hornblende crystals with their cores of augite show that the range of molecular stability of the pyroxene was exceeded and amphibole produced, possibly by the interaction of pyroxene and magma when the latter became enriched in fluxes. The large amount of combined water in the fresh appinite analysed is noteworthy in this connection.

Passing next to the granophyre, we find no visible junction with any of the other types, but the external form of the offshoot seems to indicate that it is intrusive into the main mass. The granophyre may, perhaps, represent in bulk the residual magma of the appinite with brown hornblende, the felsic portion of which it strongly resembles.

\* CAMPBELL and STENHOUSE, *Trans. Edin. Geol. Soc.*, 1908, pp. 123, 130.

† TYRRELL, *Geol. Mag.*, 1915, p. 305.

In the case of the hornblende-porphyrite and its two mineralogical modifications, the field evidence is fortunately very clear. The dyke-like mass shows well-marked chilling against members of the appinite and kentallenite groups and is therefore unquestionably younger than either. The question of the relative ages of the porphyrite and granophyre must, however, remain a matter of doubt, but the author is inclined to regard the porphyrite dyke as the younger, for it probably belongs to the latest or hypabyssal phase of Lower Devonian igneous activity, while the granophyre is of plutonic habit and texture. The minor intrusion has a N.E.-S.W. trend like most other dykes of Lower Devonian age in the district.

The sequence of rock-types in the summit complex is, therefore, given as follows:—

- (1) Olivine-basalt=kentallenite.
- (2) Appinite=hornblendite.
- (3) Granophyre.
- (4) Hornblende-porphyrite=plagiophyre=camptonite.

#### AGE AND AFFINITIES.

Three of the four main types above have been analysed by Mr W. H. HERDSMAN, and the results show all three to have unmistakable affinities with other Lower Devonian igneous rocks in Scotland.

The analysis of the orthoclase-olivine-basalt shows a close correspondence with one of a similar rock from Taynult; the Ardsheal example being, however, the fresher. This analysis has also a certain resemblance to one of the type kentallenite of Kentallen, which is not surprising in view of the close proximity of the two occurrences.

The association of high figures for potash and magnesia is the most striking point in these analyses, this being the chemical expression of rocks rich in olivine, yet containing considerable amounts of orthoclase.

The analysis of the basic appinite presents several interesting features. The surprisingly large alumina content taken with the low silica seems to indicate that the amphibole in the rock is highly aluminous. Titania, also, is high for a Lower Devonian igneous rock, and comment has already been made on the large percentage of combined water. The analysis considered as a whole does not resemble any other of neighbouring Lower Devonian igneous rocks, but it must be remembered that no analysis of an appinite has hitherto been published, and that the type is a rare and peculiar one. The analysis is quite in keeping with the mineralogical composition of the rock which is of Lower Devonian facies.

The decomposed condition of the granophyre makes any chemical analysis valueless, but it seems probable from the present mineralogical composition of the rock that in its original state it had chemical affinities with the Ballachulish "granite." The latter rock shows in places well-marked graphic intergrowth of quartz and orthoclase.

The analysis of the hornblende porphyrite is quite normal in its characters and has fairly strong andesitic affinities, the richness in feldspar and poverty in ferro-magnesian minerals being reflected in the high percentages of alumina and alkalis. An unpublished analysis of the slightly less leucocratic rock of Dundee Law (a hypersthene-andesite) is set forth for comparison.

The kentallenitic and appinitic types of the summit complex are thoroughly representative of Lower Devonian igneous activity in Argyllshire, resembling both chemically and mineralogically occurrences from neighbouring districts. The complex is one of a number of basic intrusions occurring near the Ballachulish "granite." Several of these small intrusions, hitherto unrecorded, occur on Ardsheal Hill and will be described below. Others, such as the

kentallenites of Kentallen and Achindarroch and the appinite and cortlandtite of the Allt Eilidh, have received attention in the *District Memoir*.\* In the course of an ascent of Sgorr Dhearg, the author observed several small basic bosses on the ridge running down towards Ballachulish Ferry in addition to the intrusion mapped on the 3000-feet contour. Thus it will be seen that the Ballachulish "granite" is fringed with a series of these basic intrusions—a state of affairs common in Argyllshire and of which Messrs HILL and KYNASTON write: "It is true for each eruptive area that the more basic intrusions have invaded the marginal portion, while the more acid material occupies the centre." The present writer shares the view that all the basic intrusions of the Ardsheal area are intimately connected with the Ballachulish "granite," which, along with the similar masses of Ben Nevis, Ben Cruachan, and Glen Coe, is to be reckoned as of Lower Devonian age.† It should not, however, be forgotten that boulders of a decomposed basic rock resembling kentallenite have been recorded in the base-ment conglomerate of Glen Coe.‡ The connection between the granophyre and the Ballachulish "granite" is probably even closer.

Messrs HILL and KYNASTON have described a gradual passage from augite-diorite to biotite-granite in S. Argyllshire,§ and Mr E. B. BAILEY has recorded the association of granite and cortlandtite in the Allt Eilidh;|| but Ardsheal Hill appears to be the only locality yet described where the essential contemporaneity of the appinite and kentallenite suites can be demonstrated.

## ANALYSES.

	I.	A.	B.	II.	III.	C.	D.
SiO <sub>2</sub>	50.60	49.86	48.00	40.26	60.45	58.31	60.05
TiO <sub>2</sub>	1.25	1.06	0.22	2.42	0.30	0.87	0.42
Al <sub>2</sub> O <sub>3</sub>	14.67	16.33	12.52	15.74	19.89	16.97	18.55
Fe <sub>2</sub> O <sub>3</sub>	2.81	3.62	8.74	3.44	1.76	1.45	0.93
FeO	6.47	4.34		7.95	2.27	4.42	3.41
MgO	7.04	7.80	15.26	12.09	1.54	4.09	3.46
CaO	10.05	6.47	7.94	12.03	4.04	5.66	5.44
Na <sub>2</sub> O	3.13	3.42	3.11	2.25	4.77	3.80	3.84
K <sub>2</sub> O	2.65	2.10	2.68	1.36	3.53	2.51	2.72
H <sub>2</sub> O—	0.30	1.25	1.36	0.48	0.45	0.70	0.05
H <sub>2</sub> O+	0.50	2.77		1.75	0.70	0.79	0.35
P <sub>2</sub> O <sub>5</sub>	0.24	0.54	..	0.04	0.23	0.51	0.29
MnO	0.23	0.40	..	0.03	tr.	0.05	0.16
CO <sub>2</sub>	nil.	0.23	..	0.03	nil.	n.d.	
S	nil.	..	..	nil.	tr.		
Total	99.94	100.29	99.83	99.87	99.93	100.14	99.94

I. Orthoclase-olivine-basalt. Ardsheal Hill summit S.E. Analyst, W. H. HERDSMAN.

A. Orthoclase-olivine-basalt. Cruach-Ard-Dhuine, Taynult. Analyst, E. G. RADLEY.

B. Kentallenite. Kentallen Quarry. Analyst, J. J. H. TEALL.

II. Appinite. Ardsheal Hill summit N. Analyst, W. H. HERDSMAN.

III. Hornblende-porphyrte. Ardsheal Hill summit S.E. Analyst, W. H. HERDSMAN.

C. Hypersthene-andesite. Dundee Law. Analyst, F. WALKER.

D. Hornblende-biotite-granodiorite. Ballachulish, Kentallen Quarries. Analyst, W. H. HERDSMAN.

\* *Op. cit.*, p. 172.

† The age of the local igneous activity is fully discussed in the *District Memoir*, pp. 89–92.

‡ *Mem. Geol. Survey*, Sheet 53, pp. 97, 139.

§ *Op. cit.*, pp. 544–5.

|| *Op. cit.*, p. 139.



The hornblende-porphyrity, together with a few subacid intrusions described below, is regarded as belonging to the last or hypabyssal phase of Lower Devonian igneous activity, but resembles no other porphyry in the immediate vicinity.

## SPECIFIC GRAVITIES.

Orthoclase-olivine-basalt . . . . .	3.00
Basic appinite . . . . .	3.19
Hornblende-porphyrity . . . . .	2.64

## OTHER PLUTONIC INTRUSIONS.

*Granodiorite*.—A small boss of diorite, measuring 400 yards along the N.E.–S.W. or major diameter of its lenticular outcrop, is recorded on the maps of the Geological Survey as occurring  $\frac{1}{2}$  mile due N. of Duror Inn. This rock has, indeed, a dioritic appearance in the hand-specimen, but microscopic examination proves it to be a granodiorite very similar to the neighbouring Ballachulish rock. The ferro-magnesian minerals (amounting to about 20 per cent. of the whole rock) are not fresh. Much of the dark brown biotite is chloritised, while hornblende is represented entirely by chloritic pseudomorphs. The felsic portion of the rock consists essentially of andesine, which is many times more abundant than either the turbid orthoclase or clear quartz which occur interstitially in approximately equal proportions. Apatite in large needles is a conspicuous accessory. The writer is inclined to assign a smaller area to this intrusion than has been allotted to it in the published maps.

*Augite-diorites*.—Three small bosses of augite-diorite which appear to be unrecorded were detected on the eastern slopes of the hill. The largest of these is well exposed in the burn which runs down the hill and makes a right-angled turn to the north at a point some 300 yards north of Lagnaha Farm. The boss occurs between the 200-feet and 400-feet contours.

The two other bosses of augite-diorite lie about 100 yards to the S.W. of the top and bottom of the boss in the burn, forming boulder-clad knobs on the hillside. All three bosses are composed of coarse-grained and rather decomposed augite-diorite in which augite and biotite are conspicuous in the hand-specimen. Under the microscope these minerals are seen to be equally prominent, making up together about 50 per cent. of the rock. The augite occurs as large well-formed crystals, often over  $\frac{1}{8}$  inch across, which are frequently altered to amphibole or chlorite. The biotite is seen to form large ragged flakes sometimes altered to chlorite or carbonates and occasionally ranged tangentially round the pyroxene or feldspar. Decomposed plagioclase is the only other constituent of importance, but a small amount of interstitial orthoclase and quartz may occasionally be observed, while in one section pseudomorphs after olivine occur. The boss in the burn contains irregular pink-coloured segregation veins which are made up essentially of oligoclase and microperthite, and are accordingly of syenitic composition. Modifications consisting of a more felspathic augite-diorite are also to be seen, especially towards the upper end of the intrusion. In these, quartz and alkali feldspar become much more abundant, while the ferro-magnesian minerals dwindle to unimportance.

The rock of these three intrusions strongly resembles that of the boss at Rudha Mor which is well exposed on the shore.\* Here, again, irregular pink segregation veins occur which are more abundant than in any of the other augite-diorites of the district, and primary hornblende makes its appearance sparingly.

\* *Mem. Geol. Survey*, Sheet 53, p. 155.

*Kentallenite*.—A little below the 200-feet contour, the burn which dissects the augite-diorite boss described above forms a waterfall, at the bottom of which was detected a very small unrecorded boss of kentallenite. The rock of this intrusion is exactly similar, both in the hand-specimen and under the microscope, to that of the type occurrence at Kentallen,\* 1 mile to the north. The Ardsheal boss has, however, a well-marked chilled margin in which skeletal crystals of magnetite are conspicuous, while the other minerals are almost entirely decomposed.

*Porphyrite Dykes*.—Several unrecorded dyke-like masses of porphyrite were observed at various points on the eastern slopes of Ardsheal Hill, their positions being indicated on the Sketch map. The rock of these dykes is white in the hand-specimen and contains sparse but well-formed phenocrysts of plagioclase showing lamellar twinning. Under the microscope these phenocrysts are seen to be composed of turbid oligoclase. They are set in a matrix of small stumpy laths of oligoclase and interstitial quartz. A few smaller phenocrysts of biotite, usually chloritised, or bleached, form the only coloured constituent of the rock, which may be termed quartz-biotite-porphyrite.

The trend of one of these dykes is clearly seen to the N.E.-S.W. like that of the hornblende-porphyrite in the summit complex, and one of them appears to cut the lower end of the augite-diorite boss in the burn. All these porphyrites are probably representative of the last phase of igneous activity in the district.

#### SUMMARY.

The summit of Ardsheal Hill is composed of a small igneous complex containing the following rock types intruded in the order given:—

- (1) Orthoclase-olivine-basalt=porphyritic kentallenite.
- (2) Appinite=hornblendite.
- (3) Granophyre.
- (4) Plagiophyre=hornblende-porphyrite=camptonite.

The approximate contemporaneity of the appinite and kentallenite suites may be demonstrated in this complex. Other intrusions of augite-diorite, granodiorite, kentallenite, and quartz-biotite-porphyrite from the lower slopes of Ardsheal Hill are described.

Chemical analyses show the rocks of the summit complex to be of Lower Devonian affinities, and all the other intrusions described are assigned to this period of igneous activity.

#### ACKNOWLEDGMENTS.

In preparing this paper the author owes much to the kind assistance of Mr A. M. COCKBURN, B.Sc., his former collaborator, and to the valuable advice of Dr R. CAMPBELL. Grateful acknowledgment is also expressed to the Carnegie Trust for the Universities of Scotland for a grant which allowed two rock-types to be analysed.

\* *Op. cit.*, p. 170.

## EXPLANATION OF PLATE.

Fig. 1. Olivine-orthoclase-basalt, 100 yards S.E. of Ardsheal Hill summit. A phenocryst of fresh olivine near the centre of the field shows a black reaction rim and is surrounded by phenocrysts of augite showing zoning. A few microphenocrysts of pyroxene and olivine are seen in the groundmass in which small laths of plagioclase are conspicuous.  $\times 25$  diameters.

Fig. 2. Kentallenite from boss 300 yards N. of Lagnaha Farm. Rounded crystals of olivine occur in the N.W. quadrant of the field, while large idiomorphic crystals of augite are seen near the margin. The dark brown biotite has photographed as black.  $\times 25$  diameters.

Fig. 3. Hornblende-porphyrity from dyke in summit complex. A group of hornblende phenocrysts near the centre is set in a turbid matrix in which small flakes of partly chloritised biotite may be detected.  $\times 20$  diameters.

Fig. 4. Basic appinite from the extreme north of the summit complex. Large crystals of greenish-brown hornblende occasionally show cores of clear pyroxene and inclusions of darker biotite.  $\times 20$  diameters.

Fig. 5. Edge of porphyrite dyke in summit complex. Hornblende-porphyrity in lower half of field shows well-marked chilling against coarse basalt in the upper half.  $\times 25$  diameters.

Fig. 6. Edge of porphyrite dyke in summit complex. Hornblende-porphyrity in lower half of field shows well-marked chilling against appinite in upper half.  $\times 25$  diameters.

All photomicrographs taken in ordinary light.





MR FREDERICK WALKER ON THE "IGNEOUS GEOLOGY OF ARDSHEAL HILL, ARGYLLSHIRE."

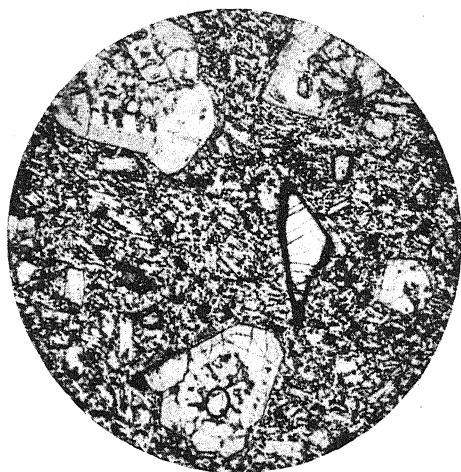


FIG. 1.

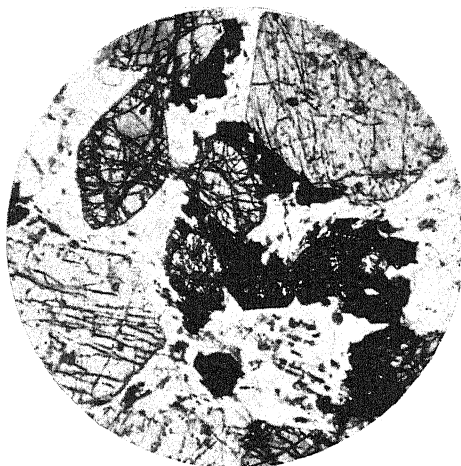


FIG. 2.

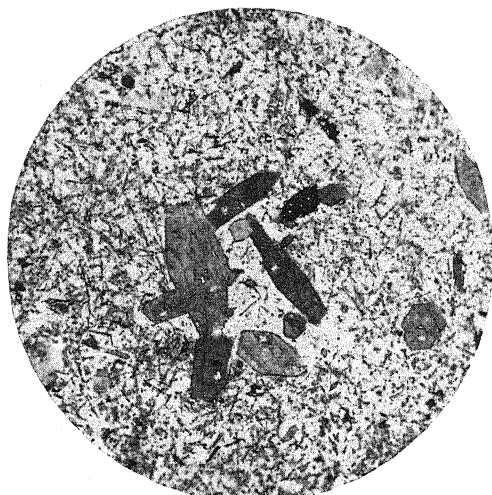


FIG. 3.



FIG. 4.



FIG. 5.

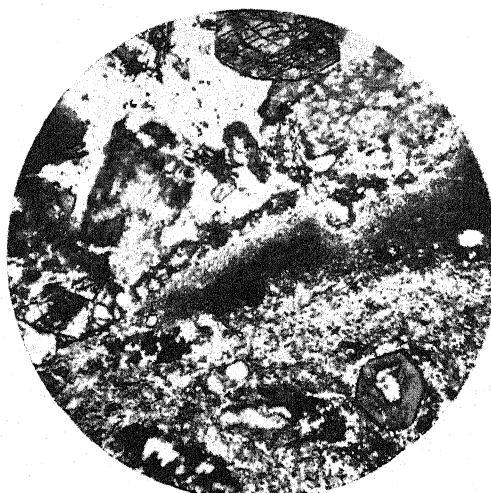


FIG. 6.





VIII.—On a Tetracotyle (*T. phoxini*) in the Brain of the Minnow. By Professor J. H. Ashworth, F.R.S., and Janet C. W. Bannerman, B.Sc. (From the Department of Zoology, University of Edinburgh.) (With One Plate and Eight Text-figures.\*)

(MS. received October 18, 1926. Read November 8, 1926. Issued separately February 12, 1927.)

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INTRODUCTION.

During the course of experiments on the toxic effects of tetrachlorethane on minnows, *Phoxinus phoxinus* (L.), Mr J. WILSON DOUGAL, B.Sc., found "cellular bodies" in a portion of the brain tissue of a dead minnow which he had spread on a microscopic slide. Sections of the head of the minnow were subsequently made by Mr RICHARD MUIR and submitted to me for an opinion on the nature of the bodies. Examination showed that they were immature Trematodes of the family Holostomidæ. I handed the sections and a living minnow, sent at the same time (May 1923), to Miss BANNERMAN for further study, remarking that the only Trematode hitherto recorded as occurring in the brain of fresh-water fish in Britain was a Tetracotyle in the brain of the lamprey and the ammocete. I subsequently directed her attention to MATARÉ's account (1910) of a similar worm which had been found in the brain of minnows collected in Switzerland and in Germany. Miss BANNERMAN studied numerous examples of the parasite during June and July 1923 and in September 1925, but she had to leave in October 1925, before the work could be completed, to take up a post in India. The comparison with previously recorded species of Tetracotyle, the discussion on the morphology of the ventral sucker, the account of the excretory canals, and a number of details in other parts have been added since she left.—J. H. A.

MATERIAL AND METHODS.

In June and July 1923 minnows (about a dozen altogether) were obtained on two occasions from a stream about five miles west of Edinburgh, and numerous Tetracotyle were found in all the specimens. A stickleback collected in the same stream was not infected. In July and August 1925 twenty-four minnows from the same area were examined with negative results, but infected fish were again obtained there in October 1926. Minnows collected in September 1925 in a small stream which flows into the north-west end of Loch Lubnaig, Perthshire, were found to contain Tetracotyle conspecific with the Edinburgh examples. Some of these were the same size as the previous specimens, but others were smaller and less developed, and had probably entered the host comparatively recently.

\* The cost of preparation of the text-figures and photomicrographs has been met by a grant from the Earl of Moray Endowment of the University of Edinburgh. The cost of preparing the line blocks and the plate, and of the copies of the latter, has been defrayed by the Carnegie Trust for the Universities of Scotland.

Two or three dozen infected minnows have been kept in running tap water in the laboratory, some of them for more than six months. They appear quite healthy, and no modification in their reactions or in their swimming movements has been observed.

The fish were killed by decapitation, and the brain was exposed and examined under a binocular microscope. Most of the Tetracotyle have been studied alive in water, sometimes with the addition of neutral red or methylene blue. Others were fixed in Flemming's fluid (strong formula), in warm Bouin's fluid, or in warm sublimate-acetic mixture, and stained as whole mounts (which, however, do not afford much help), or cut in serial sections in the three cardinal planes. Fixation by means of lactophenol, and progressive clearing in this medium while the specimen was kept under observation with a 3-mm. dry lens, proved helpful in differentiating the nervous system and other structures. Serial sections of the brain of three minnows with the worms *in situ* have also been studied.

As observed under a binocular dissecting microscope, the brain of the infected fish was of normal appearance, except that a number of the Tetracotyle could be seen as whitish oval bodies lying just under the investing membrane (the pia mater) of the mid- and hind-brain, chiefly in the lateral portions, and in most cases the fourth ventricle was crowded with them (Plate, fig. 1). Tetracotyle were not observed in the fore-brain or in the spinal cord, and examination of the eyes gave negative results; but a few worms were seen in the cranial cavity. Sections show that the great majority of the worms occur in the optic lobes, in the Sylvian aqueduct, and in the fourth ventricle (fig. 1), and the epithelial lining of these parts has undergone an extensive proliferation and has formed a vacuolated tissue (fig. 2). This appears to be the principal result of the presence of the parasites. While a few of the worms lie in the lumen of one or other optic lobe, or of the aqueduct, or of the fourth ventricle, most of them are situated in the vacuolated tissue. Usually each worm is surrounded by this tissue, but where the worms are abundant adjacent ones are not always completely enveloped and separated from one another. There is no evidence of movement of the worms in this tissue. Worms which lie between the pia mater and the brain appear to produce little disturbance beyond some displacement of the nervous tissue; in only two or three cases does the neighbouring nervous tissue seem to be adversely affected. A few worms are present in the intervals between the lobes of the brain, *e.g.* between the optic lobes and the cerebellum (fig. 1), and these are apparently free to move.

About forty infected minnows have been examined. In some of the fish only a few worms were present, in the majority several dozen were found, and in one case 247 worms were counted.\* An even greater number is present in one of the brains cut into serial sections, for one horizontal section, 10 $\mu$  thick, exhibits 70 Tetracotyle. In general, older minnows are more heavily parasited, due probably to successive infections.

#### DESCRIPTION OF THE TETRACOTYLE.

On extraction from the brain the Tetracotyle becomes active, executing creeping movements by the agency of the adhesive organs with which the ventral surface is amply provided. This surface is usually concave and the dorsal surface convex. The form of the worm is variable, especially at its anterior end. The hind part of the body forms a more or less distinct region, in which the conspicuous excretory vesicle is situated. A typical extended example is shown in text-fig. 1, but the animal is sometimes

\* This fish was 60 mm. long and is the only one which died in captivity. The cause of death was a large *Ligula intestinalis*, 90 mm. long, in the body cavity, which had for about four weeks caused great distension of the belly of the fish.

almost flask-shaped when the anterior end is well extended, or exhibits the form shown in text-figs. 2 and 7 when partially contracted, while a fully contracted example is nearly circular in outline.

The anterior end, when fully extended, is trilobate; the large middle lobe is formed by the oral sucker, and the two lateral ones by the lateral adhesive organs, which are characteristic of Tetracotyle. In retraction the anterior end assumes a rounded outline. The length and shape of the hind body depend chiefly on the condition of the excretory vesicle; when this is fully expanded the form of the hind body is as shown in text-fig. 1, but as the vesicle discharges its contents the hind region becomes shorter and more rounded in outline (text-fig. 7).

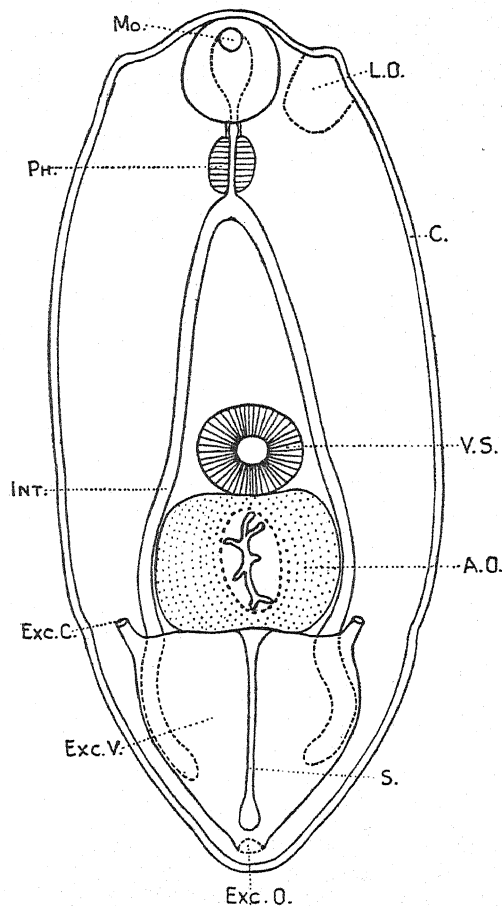
Twenty-three specimens obtained in 1923 were measured alive, the cover-glass being supported so as to avoid compression of the larvæ. Three of them were distinctly smaller than the rest, their length being  $\cdot 27$  to  $\cdot 31$  mm.; the others ranged from  $\cdot 33$  to  $\cdot 42$  mm. in length and from  $\cdot 17$  to  $\cdot 24$  mm. in breadth; the average length and breadth of these twenty examples were  $\cdot 355$  mm. and  $\cdot 185$  mm. respectively.

In September 1925 a few smaller larvæ were obtained; they were not actually measured, but the smallest were estimated to be about one-third the length of the usual examples. Half a dozen minnows, collected at the same time and in the same area, were kept in the laboratory and examined in February and March 1926, but no small larvæ were found—if any had been previously present they had no doubt had time to grow to the usual size. Those then examined were on the average  $\cdot 38$  mm. long and  $\cdot 17$  broad, and the largest example was  $\cdot 42$  mm. long and  $\cdot 2$  mm. wide.

As MATARÉ has described in considerable detail the external features and internal structure of a larva which, though smaller, appears to be otherwise closely similar to and is probably specifically identical (p. 168) with ours, we have restricted our account to a record of additional details and of those observations which are not fully in accordance with his.

The *oral sucker* is usually oval and the antero-posterior diameter (about  $\cdot 06$  mm.) distinctly longer than the transverse, but in other cases the two diameters are almost equal (about  $\cdot 05$  mm.).

The nature of the *lateral organs* was discussed at some length by MATARÉ, who concluded that they have two functions—taste and adhesion. The sensory nature of the organs is clearly indicated by their ample nerve-supply, for each receives one or two stout nerves from the cerebral mass (text-fig. 7). In life their movements recall those of the sensory lobes at the antero-lateral angles of many Triclad Turbellaria, and they may be tactile as well as gustatory. The suctorial function of these organs may be inferred from their musculature, for muscle

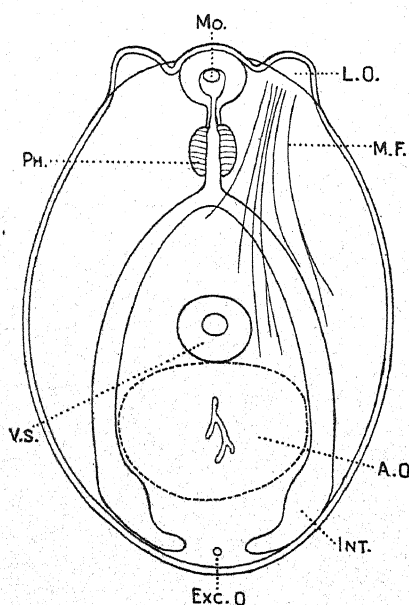


TEXT-FIG. 1.—A fully extended living specimen, observed from the ventral aspect, without pressure. Only the terminal parts of the two chief excretory canals (Exc. C.), as they open into the vesicle (Exc. V.), are represented. The internal extent of one of the lateral suctorial organs (L.O.) is indicated by dotted lines. A.O., adhesive organ; C, cuticle; Exc. O., excretory opening; Int., intestine; Mo., mouth; Ph., pharynx; S., septum; V.S., ventral sucker.  $\times$  about 300.



strands are inserted into the base of each organ and pass backwards, spreading fanwise, to their origins on the ventral body-wall, most of which are in the region of the ventral sucker, but a few are even further back. The mere retraction of the sense organ would not appear to require such a well-developed musculature, so that an adhesive function is probably correctly attributed to the lateral organs. The organ is shown in the extended and in the retracted condition in text-figs. 2 and 7 respectively.

In the middle region of the ventral surface are two more powerful adhesive organs. The more anterior is cup-shaped and has thick muscular walls, and is generally designated the *acetabulum* or *ventral sucker* (text-fig. 1). Its outline is either circular and about .06 mm. in diameter or more usually slightly oval, the longer axis being transverse. The lumen of



TEXT-FIG. 2.—A partly contracted compressed specimen, drawn from life, dorsal aspect. The lateral suctorial organs are extended; some of the retractor muscles (M.F.) of the right organ are indicated; the excretory vesicle, which was almost empty, is not represented. Reference letters as in text-fig. 1, p. 161.  $\times 180$ .

the more posterior *adhesive organ* is deep and narrow, and its chitinous lining is raised in the region near the aperture into numerous rows of ridges. Its aperture may be a simple slit, but more often is tri-, quadri-, or multi-radiate (text-figs. 7, 2, 1). The muscular wall of the organ is enveloped by a mass of gland cells—the transverse diameter of the entire organ being about .09 mm. and the antero-posterior diameter about .06 mm. Any contraction of the specimen tends to increase the transverse diameter of this adhesive organ and of the ventral sucker at the expense of the antero-posterior diameters. The adhesive organ can be completely everted, as the photograph (fig. 2) shows. In addition to this example we have seen three living specimens with the organ everted; in all the others it was retracted. Muscle fibrils arise from the dorsal body-wall and are inserted into the base of the organ; they serve for enlarging its lumen and also as retractors. This organ is the ventral adhesive organ (Haftorgan or Haftapparat).

ODHNER (1913) concluded from his studies, especially on *Cyathocotyle*, that the Haftorgan in this genus and in the Holostomes in general is derived from and is to be considered as homologous with the ventral sucker of the Distomes. In *Cyathocotyle* there is, anterior to the Haftorgan, a small sucker which he regards as an accessory structure just making its first appearance as a feebly-developed rudiment. In ODHNER'S view this is homologous with the ventral sucker of Holostomes, and the latter is therefore to be regarded as phylogenetically new and not derivable from the ventral sucker or acetabulum of Distomes.

FAUST (1918) described a median sagittal section of *Tetracotyle iturbei* in which he observed genital canals, one of which was stated to open "just in front of the acetabulum." FAUST argues that "the genital canal opening thru the anterior ventral sucker proves this sucker to be a modified genital pore," and "on the basis of this direct evidence this sucker is to be regarded as the primitive genital pore of all tetracotyle and diplostomulum larvæ, even when the connection with the genital organs has been lost." He also describes the vagina, remarking that this organ is not usually found in the holostome group.

We venture to suggest that a better figure than FAUST'S fig. 5 should have been provided in support of an argument which seeks to establish important homologies such as those in question. Moreover, the anterior genital canal described as opening "just in front of" or

"thru" the acetabulum is not shown in his figure (fig. 1) of the reproductive system, nor is the vagina represented in this figure.

SZIDAT (1924) has given special attention to FAUST's view; he figures in a median section of *Tetracotyle typica* (for comparison with FAUST's fig. 5) a narrow passage which, he points out, is nothing more than the narrow lumen, ending blindly, produced by folding of the wall of the Haftorgan. He further states that the organ interpreted by FAUST as the vagina is the large glandular organ associated with the Haftorgan.

We have carefully examined the serial sections of our *Tetracotyle*, and can state definitely that, as genital ducts are not yet developed, there are no such ducts associated with either of the ventral suckers. This in itself is, of course, not an argument against FAUST's view, for he was dealing with another species in which the reproductive apparatus appears to be different in more than one respect. But FAUST's unconvincing figure and SZIDAT's criticism and alternative interpretation thereof lead us to the conclusion that, on the evidence available, there is not justification for changing the designation "anterior ventral sucker" to "primitive genital pore." Until further comparative observations enable a definitive terminology to be agreed upon, it will be convenient to continue to designate the two suckers respectively as "anterior ventral sucker" and "ventral adhesive organ" or "Haftorgan."

The ample provision of adhesive organs in *Tetracotyle*, together with the arrangement of certain of the body muscles, described by MATARÉ, emphasises the importance of the sucking reflex in this worm.

The *cuticle* which covers the entire surface of the worm is smooth—that is, has no spines. It is barely  $5\mu$  thick, and exhibits two layers which are readily differentiated both in life and in stained sections. The outer layer is slightly thicker than the inner, stains more deeply, and is marked with fine striations perpendicular to the surface. On examining it in living specimens lightly stained with neutral red, this outer layer is seen to be marked out into minute, close-set, hexagonal areas, as described by MATARÉ. The inner layer of the cuticle is a homogeneous or very finely granular film which stains faintly.

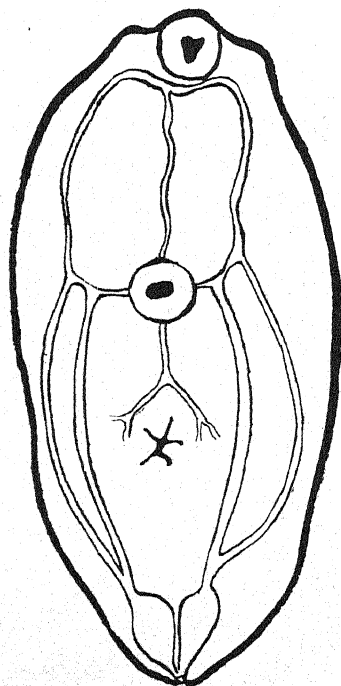
We have nothing to add to MATARÉ's account of the muscular system, the parenchyma, and the alimentary canal, with the exception of the *intestine*. He states that the two limbs of the intestine extend to the posterior end of the body, and that just in front of their blind ends they are bent at a right angle. In our living examples, examined without pressure, each limb of the intestine can be seen lying dorsal to the excretory vesicle, and can be traced rather more than half-way along the latter, where its blind end is situated (text-fig. 1). The terminal portion of the intestine is curved medially. In examples in which the contents of the excretory vesicle have been partially discharged, the inward curvature of the terminal part of the intestine is more marked (text-fig. 2), and in many preserved specimens the intestine exhibits a right-angled bend (text-fig. 7).

MATARÉ states that the limbs of the intestine are of purely epithelial nature. He suggests that as the gut walls are in very close connection with the parenchyma, the movement of the intestinal contents is probably brought about by the parenchymal musculature.

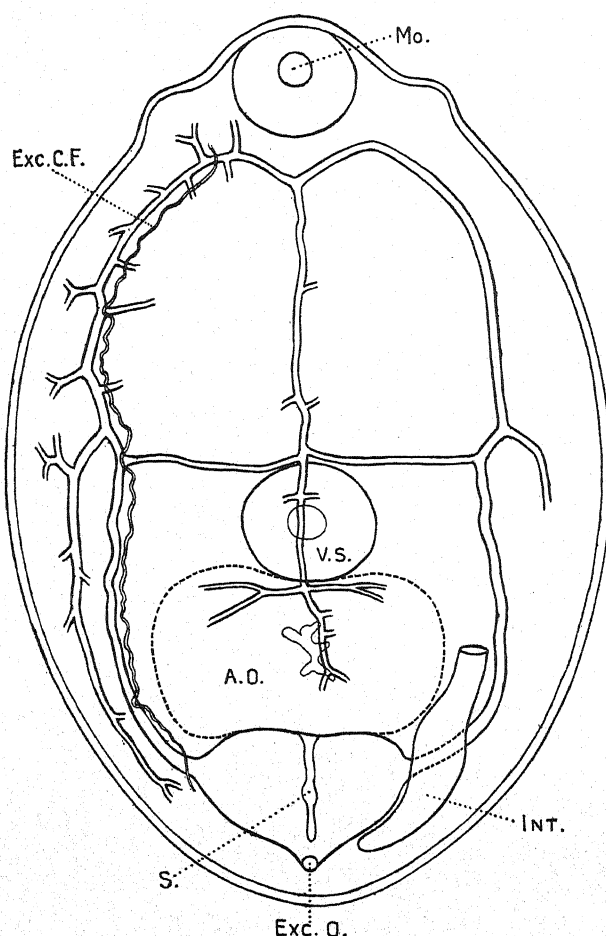
In our horizontal series of sections we have found fine, circular, muscle fibrils—close set, being only about  $1\mu$  apart—in the wall of the intestine, and longitudinal fibres are also present. The movement of the contents is therefore explicable without reference to the parenchymal muscles. The gut contents, which stain red with neutral red and are therefore acid, consist of a fluid in which are numerous brownish spherules, chiefly 2 to  $3\mu$  in diameter, no doubt the remnants of the digestion of blood which, with the cerebral fluid, appears to form the food of the larva. In a few examples we have seen a cell or two of the vacuolated

ependyma in the oral sucker, and possibly that tissue may also form part of the food of the worm.

MATARÉ devoted considerable attention to the *excretory system*, the study of which is difficult owing to the presence of highly refractive spherules (concretions) in the blind ends of most of the excretory tubules. These spherules present concentric layers and attain a diameter of 7 or 8 $\mu$ , or occasionally 10 $\mu$ . We have spent much time in the endeavour to trace



TEXT-FIG. 3.—To show the principal canals of the excretory system according to MATARÉ (1910, p. 528).



TEXT-FIG. 4.—To show the principal canals of the excretory system. Drawn from a living, slightly compressed specimen, dorsal aspect. The excretory vesicle had discharged part of its contents. The suckers are seen through the animal. The terminal portion of the right limb of the intestine is represented. Exc. C.F., fine excretory canal which receives tributaries from flame-cells. Other reference letters as in text-fig. 1, p. 161.  $\times 300$ .

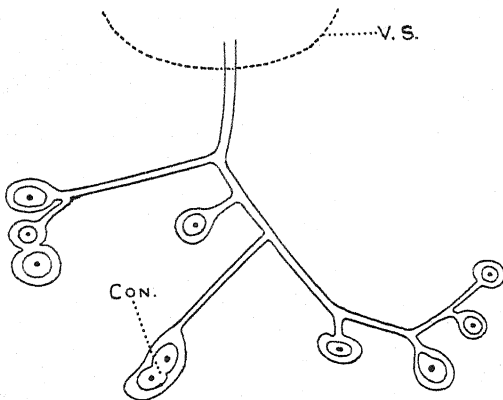
the excretory canals, because we found that our observations did not agree in one important point with those of MATARÉ, and we have therefore been particularly careful to confirm our findings in this respect. His figure of the main vessels of the excretory system is reproduced in text-fig. 3; our interpretation of the arrangement of the vessels is shown in text-fig. 4. The essential difference is that we find one principal excretory vessel entering the vesicle on each side, whereas he shows two main vessels uniting to form one common trunk. It is, of course, possible that we are dealing with a different species and that both accounts are correct; but realising from our experience the great difficulty in tracing the course and origin of the lateral canal which arises from two tributaries situated almost against the wall of the vesicle,



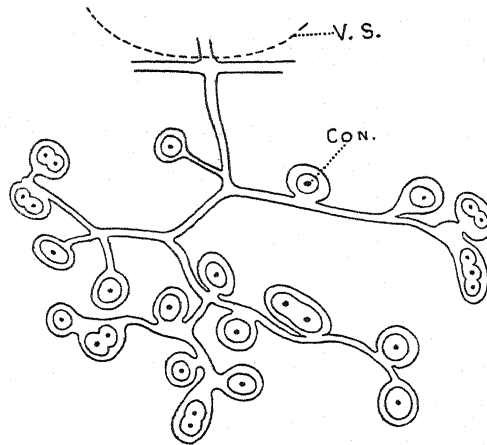
we think it probable that the arrangement we have figured may have been that present also in MATARÉ's specimens.

That a single chief canal on each side opens into the vesicle in our examples was demonstrated time after time both by direct observation of the course of the more lateral canal, which proved that it opened into the chief canal, and also by drawing small amounts of lactophenol under the cover-glass towards the preparation and observing the stages of contraction of the vesicle. As the vesicle began to diminish in size, the connection of its antero-lateral angles with one canal only became fully evident.

The *chief excretory canal* of each side is formed by the union of an anterior and a posterior canal at a point almost equidistant from the anterior and posterior ends. From this point the main canal runs for a short distance obliquely in a postero-medial direction and receives a transverse commissural vessel, after which it runs backwards nearly parallel to the lateral margin of the body until it reaches the posterior margin of the Haftorgan, where it curves



TEXT-FIG. 5.—The median portion of the dorsal excretory canal, which lies posterior to the ventral sucker (V.S.). CON., concretion.  $\times 600$ .



TEXT-FIG. 6.—A corresponding portion from another specimen.  $\times 600$ .

medially and opens into the antero-lateral angle of the vesicle. The two anterior canals are connected in front, immediately posterior to the oral sucker, and at their point of union is received a median dorsal vessel, which can be traced backwards dorsal to the ventral sucker and Haftorgan nearly to the level of the vesicle, where it is formed by tributaries which come from the small sacculi containing concretions (text-figs. 5, 6).

While there is a fair agreement in different specimens as to the number and relations of the principal tributaries of the excretory system, variation is exhibited by the smaller tributaries. For instance, the portion of the median dorsal vessel behind the ventral sucker may have the comparatively simple form shown in text-fig. 5, or present the more elaborate plan shown in text-fig. 6, or an intermediate condition.

The principal tributaries of the main canals are shown in text-fig. 4, and all these arise from similar sacculi. But there is also a fine canal (Exc. C.F.), not more than  $2\mu$  in diameter, which receives tributaries which arise from flame-cells. Unfortunately, the presence of the numerous concretions prevents anything like a complete elucidation of the plan of arrangement of the finer vessels and the flame-cells. In the larger examples we have observed about forty flame-cells, the majority in the posterior half of the larva; but there are almost certainly more. Their ducts discharge into the fine canal already mentioned. This can be traced from the region lateral to the oral sucker along the medial side of the anterior excretory canal and

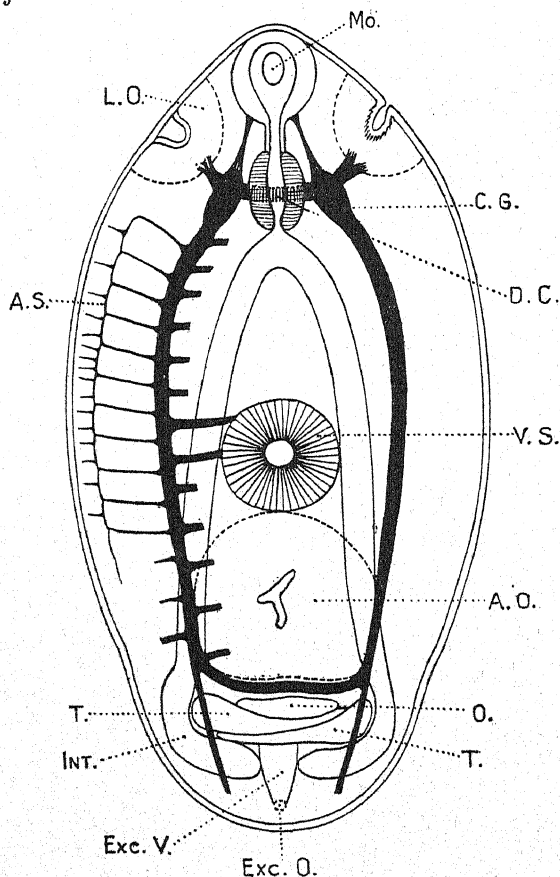
along the chief excretory canal—sometimes mesial to it, or slightly lateral to it—to a point just behind the opening of the chief canal into the vesicle. At three points on its course it

appears to be intimately connected with the larger canal, and probably opens into the latter at these places, though this was not definitely ascertained. It should be added that this fine canal was demonstrable only in very fresh specimens.

Our observations are in close agreement with those of FRAIPONT (1880) on the excretory system of *Diplostoma volvens*.

The vesicle in its state of full expansion (text-fig. 1) is about .09 to .1 mm. long and almost heart-shaped, and is traversed by a median septum which does not extend quite to the posterior end of the vesicle. The vesicle opens by a short canal through the excretory pore, which is not terminal but slightly dorsal in position.

The reproductive system is represented by three groups of cells which lie immediately posterior to the adhesive organ and dorsal to the excretory vesicle. Their relations are represented in text-fig. 7. The ovary is anterior to the two testes, the median parts of which overlap. The cells of the latter (spermatogonia) are 5 to 6 $\mu$  in diameter, their nuclei are large (about 4 $\mu$  in diameter), and in most of them the chromatin is collected into a central mass. The ovarian cells are similar in structure, but are distinctly smaller. In a few specimens the spermatogonia have undergone division.

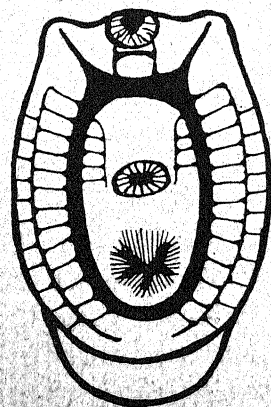


TEXT-FIG. 7.—Drawn from a preserved and cleared, but somewhat contracted, specimen, ventral aspect, to show the nervous system, gonads, and alimentary canal. The excretory vesicle is empty. The branches of the nerve cord have been added from a series of horizontal sections. A.S., "Aussenstrang" (MATARÉ) or longitudinal marginal nerve; C.G., cerebral ganglion; D.C., dorsal commissure; O., ovary; T., testis. Other reference letters as in text-fig. 1, p. 161.  $\times 300$ .

Around the ovary and around each testis is a thin cellular envelope. There are no traces of genital ducts.

For the study of the nervous system we have employed a large number of living specimens, and after making such observations as were possible thereon, we have drawn lactophenol into each preparation and observed the specimen as fixation and progressive clearing took place. At one phase the nerve cords stand out with great clearness. We have checked and added to these observations by the study of serial sections—transverse and horizontal.

The two cerebral ganglia are situated at the sides of the posterior part of the pharynx, and are connected dorsal to the pharynx by a commissure about 6 $\mu$  broad (fig. 5 and text-fig. 7). There is no ventral commissure. From each cerebral ganglion are given off: a nerve ventrally to the ventral body-wall (fig. 5); one or two stout nerves ventro-laterally, which divide fanwise in the lateral adhesive organ; a nerve to the oral sucker



TEXT-FIG. 8.—The nervous system, after MATARÉ (1910, p. 533).

(fig. 4), and one to the pharynx; two nerves to the dorsal body-wall; and a nerve cord which can be traced to the posterior end of the worm (text-fig. 7). This cord, which is oval in section, lies near the ventral body-wall and gives off branches laterally and medially at fairly regular intervals. The lateral branches are connected by a longitudinal nerve—the “Aussenstrang” observed by MATARÉ—which runs almost parallel to the lateral margin of the body. Immediately after passing the Haftorgan the nerve cords are united by a stout transverse commissure. The cord can be seen lying lateral to the excretory vesicle and traced to within  $15\mu$  of the hind end of the animal.

#### COMPARISON WITH PREVIOUSLY RECORDED TETRACOTYLE.

The name Tetracotyle has been employed in a restricted and in a wider sense. In its stricter usage it designates larvæ which, like that described in this paper, possess at each side of the oral sucker an organ which is muscular or glandular, or both, and is to a greater or less extent capable of suctorial action.

The genera *Diplostomum* and *Tylodelphys* include two other groups of Holostomid larvæ which are distinguished from Tetracotyle by the absence of the lateral suctorial organs. But some authors have employed the name Tetracotyle in a wide sense, and have included, under this designation, larvæ which should have been placed under *Diplostomum* or *Tylodelphys*. MATARÉ's list (1910, p. 496) of the known species of Tetracotyle affords an example of this practice, for, of the twenty-three species cited, more than half do not belong to the genus Tetracotyle (*s. str.*).

Much investigation is required on the structure of many of the larvæ and on their relations to adult forms—few of which are known—before the terminology can be placed on a sound basis. It would seem desirable in the meantime to employ the name Tetracotyle in the more restricted sense.

Of the recorded larvæ of Holostomidæ apparently only three agree with ours in having a smooth cuticle and a V-shaped excretory vesicle:

*Diplostomum volvens* v. Nordmann, from the eye of perch and other fresh-water fishes.

*Tetracotyle petromyzontis* Brown, from the brain of *Ammocætes*.

*Tetracotyle phoxini* Faust, from the brain of the minnow.

*Diplostomum volvens* is about .4 mm. long, that is about the same size as our Tetracotyle from the minnow, but differs from the latter in that the lateral processes at the anterior end, though partly retractile, are not capable of being converted into sucking organs. Moreover, the proportions of the suckers are different; in *D. volvens* the transverse diameter of the ventral sucker is about twice that of the oral sucker, and the adhesive organ has almost twice the diameter of the ventral sucker. In our species the transverse diameters of the oral and ventral suckers are approximately equal. The ventral sucker of *D. volvens* is slightly anterior to the middle of the body, and there is a distinct interval between it and the adhesive organ; in our species these two organs are usually in contact. The excretory vesicle and the details of arrangement of the excretory canals in *D. volvens*, as figured by FRAIPONT, are almost identical with those in our specimens. FRAIPONT states that the median septum which arises from the ventral wall of the vesicle does not reach the dorsal wall; in our examples the septum is complete, extending to the dorsal wall (fig. 6). On the ground of the structural differences cited it may be concluded definitely that our examples are not *D. volvens*. Further, the specific habitat of this species is the eye and not the brain of fresh-water fishes.

*Tetracotyle petromyzontis* has an average length of .42 mm. and possesses two antero-lateral



processes which can be converted into grooved adhesive organs. The oral sucker, ventral sucker, and adhesive organ are in fair agreement in their relative sizes and positions with those of our examples, but some of the internal structures as figured by BROWN do not conform. The two limbs of the intestine are shown (BROWN's fig. 11) terminating close to the middle line and immediately behind the adhesive organ. In the excretory system the transverse anastomosis, well-developed in our specimens, is very feebly marked (cf. BROWN's fig. 7 and our text-fig. 4), and the excretory vesicle is represented (fig. 11) as consisting of two widely separated portions, each more or less oval in form, opening through a short common portion to the exterior. BROWN states that his fig. 11 is a plan drawn from horizontal sections; the shape of the excretory vesicle has no doubt been considerably affected by contraction during preservation. We may add that in our examples the excretory vesicle, during the later phase of discharge of its contents, assumes a form similar to that figured by BROWN in *T. petromyzontis*.

*Tetracotyle petromyzontis* exhibits a general resemblance to our species, and the differences in the excretory system and in the position of the terminal parts of the intestine may be less than BROWN's figures suggest. A re-examination of fresh material of this species is necessary before its relations can be determined.

*Tetracotyle phoxini*.—MATARÉ gave a detailed account of this "neue Tetracotyle," but he did not name the species; the specific name was added by FAUST (1918). Our specimens agree in most respects so fully with MATARÉ's that it is difficult to believe they can be other than conspecific, and yet there are two features in which there is divergence. His examples were little more than half the size of ours (.2 mm. long and .15 mm. broad), but we have seen a few small examples, and the disparity in size cannot be held to be decisive. MATARÉ describes and figures two main excretory canals on each side which unite and open by a common trunk into the excretory vesicle, whereas we find only one main canal on each side. The difficulties of observation in the region concerned are, however, so considerable that we are not inclined to regard this difference as proved or as a ground for the specific distinction of our examples from MATARÉ's.

#### OTHER STAGES OF *Tetracotyle phoxini*.

In the minnows caught near Loch Lubnaig in September 1925 were *Tetracotyle* of smaller size than any found in the material of 1923. The smallest was little more than .1 mm. long and had probably only recently entered the minnow. Some of the fish of this collection were kept in the laboratory until February and March 1926, but by that time no small worms were found in them; they had all reached a length of .35 mm. to .42 mm.

It is hoped that a re-examination of the molluscs of the area—one or more of which is the first intermediate host in which the stages of development up to the cercaria, and possibly up to the *Tetracotyle*, are passed—will provide material by means of which the mode of entry of the parasite into the minnow (the second intermediate host) and the route to the brain can be established. The host in which the worm attains maturity is unknown.

#### THE DISTRIBUTION OF *Tetracotyle phoxini*.

MATARÉ's original examples were obtained from minnows from the Lenzer Heide, about eight miles south of Chur, Grisons, Switzerland, but he subsequently found the same species in minnows collected in the neighbourhood of Munich.

We first observed British examples of *T. phoxini* in minnows obtained in May 1923

from a stream five miles west of Edinburgh, and other minnows infected with the same species of *Tetracotyle* were collected in the same area in October 1926. In 1925 minnows caught in a stream flowing into Loch Lubnaig, Perthshire, were found to harbour *T. phoxini*.

Through the kindness of Dr NELLIE B. EALES one of us has been enabled to examine two collections of minnows from the neighbourhood of Reading. The first examples were sent in July 1926, and proved to be only lightly infected. The worms were alive, though not active, when they arrived in Edinburgh. No difference between them and the Scottish examples could be detected; in their form and size ( $\cdot 3$  to  $\cdot 42$  mm. long), in the relative position and proportion of their suckers, and in the arrangement of the main excretory canals, they conformed to the description given in the earlier part of this paper. The second series of minnows, sent early in October 1926, were more heavily infected. The *Tetracotyle* were in better condition, and careful examination afforded confirmation of the view that the Reading and the Scottish examples belong to the same species.

Professor A. E. BOYCOTT, F.R.S., has kindly sent to one of us sections of the head of a minnow, collected at Radlett, Herts, in the brain of which are several *Tetracotyle*. These agree in size and, so far as can be ascertained from sections, in structure with those described in this paper. While it is impossible definitely to identify them as *T. phoxini*, they probably belong to this species.

#### PREVIOUS RECORDS OF THE OCCURRENCE OF HOLOSTOME LARVÆ IN THE BRAIN OF FISHES.

In 1839 JOHANNES MÜLLER recorded the presence of a mass of small Entozoa, agreeing in size and form with HENLE's *Diplostomum rachiceum*, in the fourth ventricle of *Lampetra* (*Petromyzon*) *fluviatilis*. In 1850 DIESING (p. 307) referred to this Entozoon as a "species nondum descripta"—"*Diplostomum Petromyzi fluviatilis*," but in 1858 (p. 316) he cited it as "*Tylodelphys? Petromyzonis fluviatilis*." In 1870 GULLIVER found that in every *Lampetra planeri* from the Stour at Canterbury the brain case was occupied by a mass of living worms equal to that of the brain substance, and that the worms had an average length of  $\frac{1}{16}$  inch (i.e. about  $\cdot 4$  mm.). In a later paper (1872) GULLIVER named the worm provisionally *Neuronaia Lampetræ*, but the only further information he gave about it was that there are no spines near the mouth or on the surface of the body.

In 1899 A. W. BROWN described the structure of *T. petromyzontis* from the brain cavities of *Ammocetes* collected near Oxford. The worms were found in great numbers, mostly in the fourth ventricle.

Finally, in 1910, MATARÉ gave his detailed account of the species, named by FAUST (1918) *T. phoxini*, from the brain of minnows.

In all these cases of infection of the brain, sometimes with great numbers of the worms—MATARÉ estimated that in heavy infections 400 to 500 were present—there is no apparent effect upon the host's reactions. In none of these cases has the mode of infection been ascertained.

SZIDAT found cercariæ (his *Cercaria C.*) in the mid-brain of a *Leuciscus rutilus* which had been placed in water containing these larvæ, but the infection of the brain was apparently slight. *Cercaria C.* was shown to develop into *Diplostomum volvens*, whose specific habitat is the eye of fresh-water fishes.

In 1853 LEYDIG recorded the occurrence of several hundred Trematodes about 1 mm. long in the cranial cavity of *Cobitis fossilis*. The worms were moving freely on the brain and in the surrounding fluid. This worm, named by DIESING (1858) *Tylodelphys? craniaria*, does not appear to have been observed since.

## OTHER HELMINTHES FROM THE MINNOW.

During the course of the work on *Tetracotyle* the following Helminthes, which have apparently not been previously recorded from the minnow, have also been obtained:—

*Diplostomum* sp.—In the fourth ventricle of two minnows collected near Edinburgh (October–November 1926) a *Diplostomum*—a single specimen in each fish—was found. One example was .3 mm. long and the other .4 mm. long and .19 mm. broad. The larger one was more carefully examined. Its cuticle is very thin and smooth. The antero-posterior and the transverse diameters of the oral sucker are .04 and .045 mm. respectively, the diameter of the ventral sucker is .035 mm., and of the adhesive organ about .06 mm. There is a distinct interval between the ventral sucker (which is in the middle of the body or slightly further back) and the adhesive organ. The concretions in the sacculi of the excretory system seldom exceed  $3\mu$  in diameter, and the excretory vesicle is V-shaped. The characters of this *Diplostomum* do not agree with those of any recorded species.

*Allocreadium*.—In two other minnows collected near Edinburgh small Distomids—four altogether—were found on the liver or on the stomach. As they were unduly compressed during preparation they are not in good condition and only one of them is mature. The mature specimen is about 2 mm. in length, the others are from .7 mm. to 1 mm. long. They appear to be *A. angusticolle* (Hausmann), but the determination is given with some reserve.

*Gyrodactylus*.—The specimens are .3 to .365 mm. long and are probably *G. medius* Kathariner. They are abundant on the fins, and on the skin generally, of many of the minnows from the neighbourhood of Edinburgh and from Loch Lubnaig.

*Dactylogyrus* sp.—Several specimens about .4 to .6 mm. long have been obtained from the gills of minnows caught near Edinburgh. The armature of the posterior disc—the hooks and the dorsal and ventral chitinous supporting pieces—do not agree with those of any species figured by LÜHE (1909) or by WEGENER (1910).

*Ligula intestinalis* (L.).—The belly of one of the minnows brought to Edinburgh in September 1925 from near Loch Lubnaig was noticeably swollen in February 1926, and became more and more distended until death occurred about four weeks later. The minnow, which was 60 mm. long, had in its abdominal cavity a *Ligula* 90 mm. long.\*

## SUMMARY.

A *Tetracotyle*, which we believe to be identical with *T. phoxini* (Faust, 1918), originally described by MATARÉ (1910) from minnows (*Phoxinus phoxinus* (L.)) collected in Switzerland and in Germany, is recorded from minnows obtained from two localities in Scotland and from Berkshire and Hertfordshire in England.

The parasites have been found only in the brain, and chiefly in the cavities of the optic lobes, in the Sylvian aqueduct, and in the fourth ventricle. The epithelial lining of these cavities has undergone extensive proliferation, and forms a vacuolated tissue in which most of the worms lie.

The majority of the *Tetracotyle* were .33 to .42 mm. in length. In heavily infected examples about 250 or more *Tetracotyle* were found, but the fish were apparently quite healthy.

The view advanced by FAUST that the ventral sucker or acetabulum is to be regarded as the primitive genital pore is, in our opinion, not justifiable on the evidence cited.

\* I have another specimen of *Ligula*, 72 mm. long, found by Dr A. J. Hesse in the abdominal cavity of a minnow from Loch Lubnaig in July 1921.—J. H. A.



The intestine is not purely epithelial, as stated by MATARÉ, but possesses both circular and longitudinal muscle fibres.

MATARÉ describes and figures two main excretory canals on each side, which unite and open by a common trunk into the excretory vesicle. We find only one main canal on each side. In view of the difficulty in observing the canals in this region we are inclined to believe that the arrangement we have figured may have been present also in MATARÉ's examples. A very slender canal receives tributaries from the flame-cells; it is closely associated at three places with the main excretory canal, into which it no doubt discharges.

The immature reproductive organs—an ovary and two testes—are represented by three groups of cells, each enclosed in a thin cellular envelope; there are no genital ducts.

The two main nerve cords extend almost to the end of the body (*cf.* MATARÉ's figure).

MATARÉ's examples were little more than half the size of ours, but the agreement in most other respects is so close that we see no valid reason for considering our specimens as specifically distinct from his.

The minnow is the second intermediate host, and the Tetracotyle is an immature post-cercarial stage. The first intermediate host (a fresh-water mollusc in which the development up to the cercaria or to the Tetracotyle stage takes place), the route of the parasite to the brain of the minnow, and, finally, the host in which the worm reaches maturity, have still to be ascertained.

Other Helminthes obtained from Scottish minnows are: A *Diplostomum* from the fourth ventricle; a Distomid, referred under reserve to *Allocreadium angusticolle*, found on the liver and on the stomach; *Gyrodactylus medius* from the fins and the skin; a species of *Dactylogyrus* from the gills; and *Ligula intestinalis* from the abdominal cavity.

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## DESCRIPTION OF PLATE.

Fig. 1. Horizontal section of the optic lobes and hind brain of minnow, showing the Tetracotyle in the cavities of the optic lobes, in the Sylvian aqueduct, and in the fourth ventricle. On the left side a Tetracotyle lies in the groove between the optic lobe and the cerebellum, and further back another is seen just under the pia mater.  $\times 24$ .

Fig. 2. Portion of a section of the ventricle showing the Tetracotyle, one with its ventral adhesive organ everted, lying in the proliferated and vacuolated ependyma.  $\times 300$ .

Fig. 3. Median vertical section of a Tetracotyle lying in the hind brain immediately under the pia mater. At the anterior (left) end are the mouth (Mo.) and the oral sucker; on the ventral surface are the ventral sucker (V.S.) and the adhesive organ (A.O.), with its basal gland cells, posterior to which is the almost empty excretory vesicle and the dorsal excretory pore (Exc. O.). The deeply staining cells immediately dorsal to the vesicle are the gonads.  $\times 300$ .

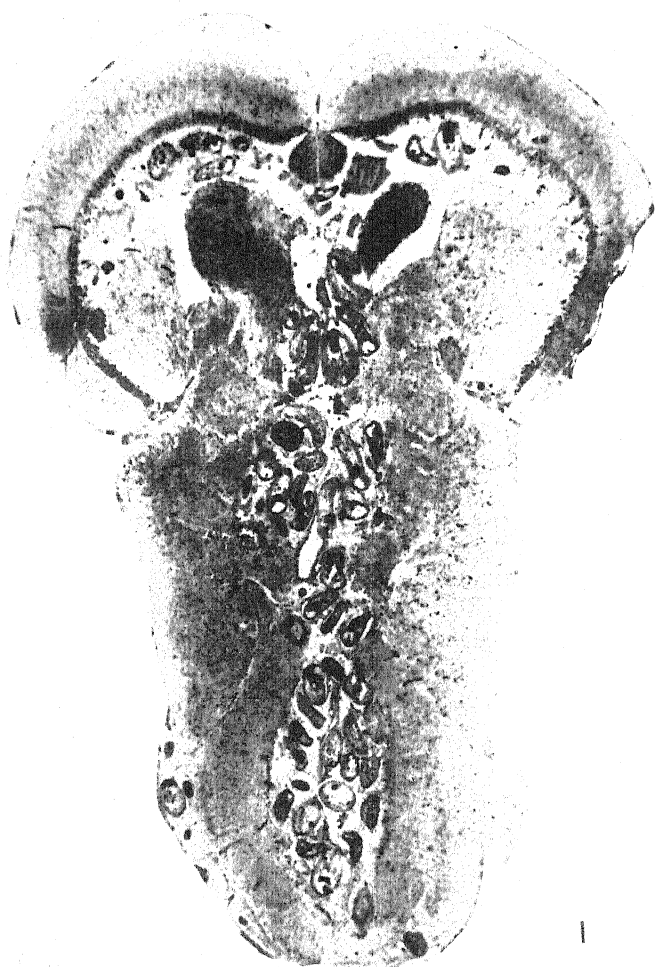
Fig. 4. Horizontal section showing outline of the oral sucker, the pharynx, and the two limbs of the intestine. Right and left of the pharynx are the cerebral ganglia (C.G.), each giving off a nerve to the oral sucker. Lateral to the intestine on each side is seen the main excretory canal; the right canal (Exc. C.) can be traced almost into the vesicle (Exc. V.). On the left side, lateral to the canal, are shown several of the terminal bulbs of the excretory system which in life contained concretions. The deeply staining cells across the middle of the worm are gland cells. A few oogonia are seen in the basal part of the septum of the excretory vesicle.  $\times 500$ .

Fig. 5. Transverse section through the pharynx, cerebral ganglia, and dorsal commissure.  $\times 680$ .

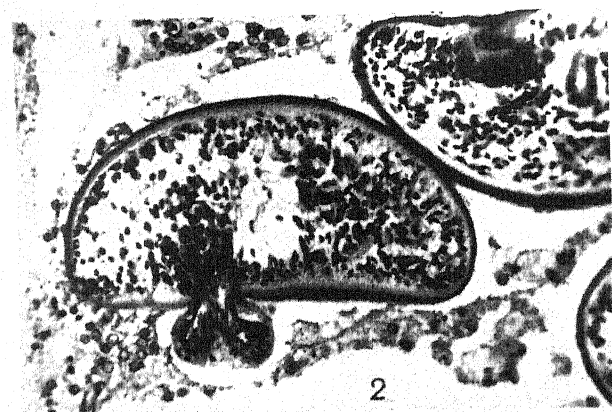
Fig. 6. Transverse section of the same specimen as that shown in fig. 5, passing through the gonads and the excretory vesicle. On the right of the excretory vesicle is the main excretory canal, and a little dorsal to it the intestine (INT.). In the dorsal base of the septum of the excretory vesicle are two or three oogonia (Oo.), and above the two halves of the vesicle are the spermatogonia (Sp.) of one of the testes.  $\times 680$ .



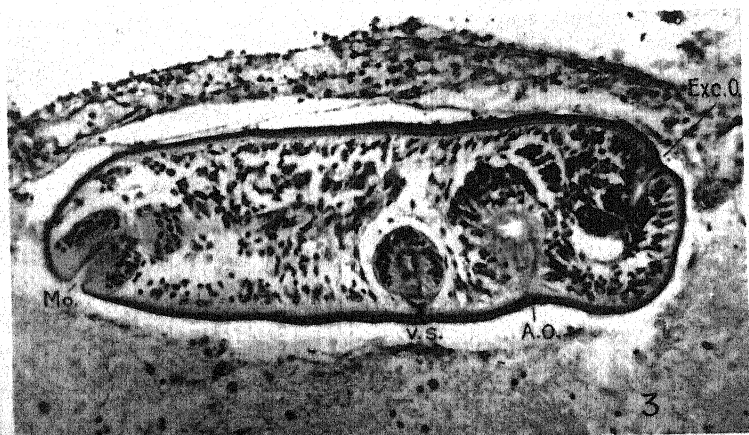
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TETRACOTYLE IN THE BRAIN OF THE MINNOW.



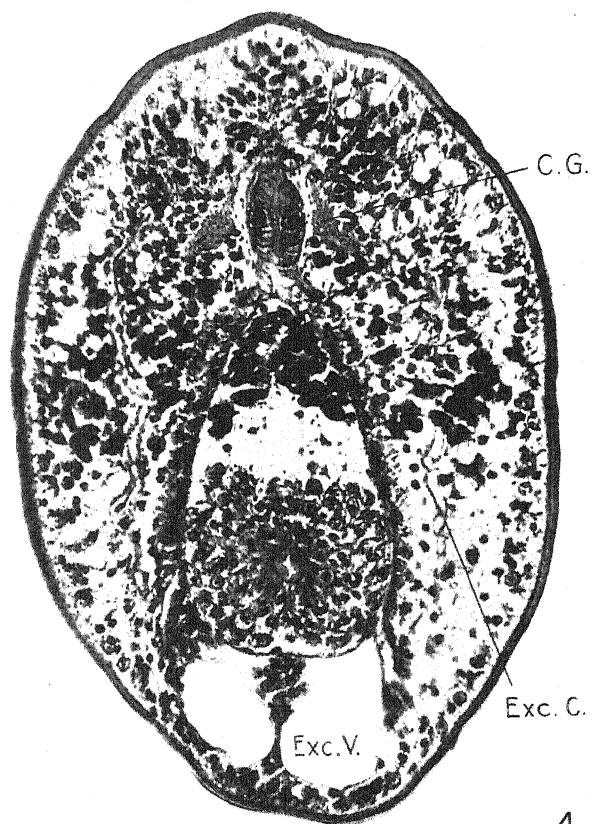
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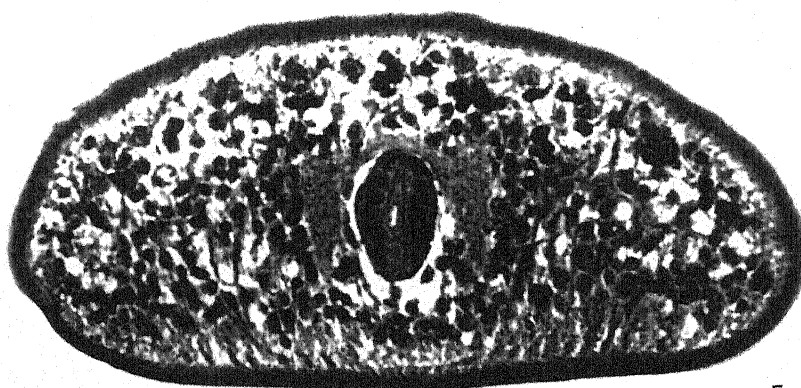
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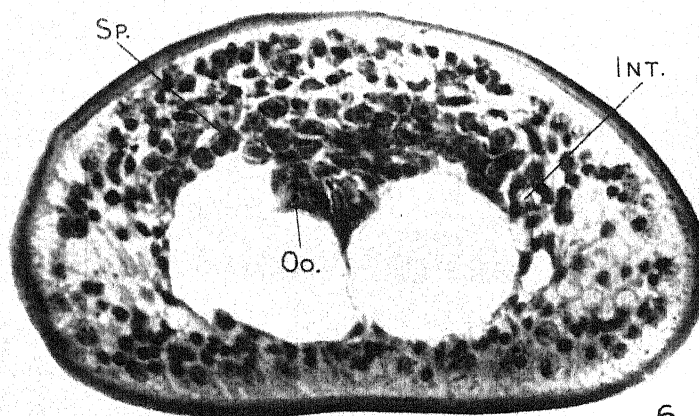
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IX.—A Critical Examination of the Vittarieæ with a View to their Systematic Comparison. By S. Williams, M.Sc., Ph.D., Lecturer in Botany, Glasgow University. (With Three Plates and Thirty-one Text-figures.)

(MS. received June 21, 1926. Read June 21, 1926. Issued separately February 21, 1927.)

The Vittarieæ, as described by CHRISTENSEN,\* comprises five genera, viz. *Vittaria*, *Monogramma*, *Antrophyum*, *Hecistopteris*, and *Anetium*, all of which are epiphytic forms growing in the damp forests of the Old and New World Tropics. All of them possess creeping rhizomes on which the fronds are arranged more or less definitely in two rows on the dorsal surface. The fronds are simple in outline, with the exception of those of *Hecistopteris* which are dichotomously branched. The venation of the fronds is reticulate, except in *Hecistopteris* where there is an open, dichotomous system of veins, and in *Monogramma*, in some species of which the venation consists simply of a mid-rib. An interesting feature, which has proved to be valuable as a diagnostic character, is the presence of "spicule cells" in the epidermis of the fronds. These spicule cells are elongated cells containing spicules of silica, and their presence appears to be universal in the Vittarieæ. The sporangia are fairly constant in form throughout the group, but their distribution is extremely varied. The roots are characteristically provided with very numerous reddish-brown root hairs, a character shared with other epiphytic Ferns. The Gametophyte is divergent from the common cordate type in all cases where it has been investigated. Such are the main external characteristics of the group under consideration.

The five genera at present included in the Vittarieæ have had an extremely varied systematic history, a fact which indicates at once that there is likely to be considerable difficulty in any attempt to consider their systematic relationships. The grouping of the genera under the name Vittarieæ is of comparatively recent date, and prior to that time the various genera received very varied treatment at the hands of the systematists. PRESL, in his *Tentamen Pteridographiæ* (1836), placed *Vittaria* and *Prosaptia* (now *Davallia*) in the Tribe Vittariaceæ. A number of *Antrophyum* species and *Monogramma* were placed in Section I, Grammitideæ of the Tribe Grammitaceæ, while the remaining species of *Antrophyum* and *Hemionitis spatulata* (now *Anetium citrifolium*) were placed in Section II, Hemionitideæ of the same Tribe. HOOKER (*Synopsis Filicum*, 1868) placed all five genera in the Tribe Grammitideæ (*Hecistopteris* being included under *Gymnogramme*), without, however, grouping the genera in any way as separate from the other forms included in the same group. In the *Historia Filicum* (1875) of J. SMITH, *Vittaria*, *Pteropsis angustifolia*, and *Dictyoxiphium* are placed in his Tribe Vittarieæ. *Monogramma*, *Diclidopteris* (now included in *Monogramma*), *Pleurogramma*, and *Hecistopteris* are placed in the Tribe Pleurogrammeæ. *Antrophyum* is placed in the Tribe Grammitideæ, although the writer states that "The general aspect and mode of growth indicates the affinity of this genus to be with *Vittaria*." GOEBEL † suggested in 1896 that the five genera should be placed together in the Vittarieæ. This suggestion was based on the characters of the gametophyte and on certain characters of the sporophyte, chiefly the presence of spicule cells in the epidermis of the fronds. GOEBEL's suggestion was followed by CHRIST (*Die Farn-*

\* CHRISTENSEN, *Index Filicum*, 1906.

† GOEBEL, "Hecistopteris, eine verkannte Farn-gattung," *Flora*, 1896.

*kräute der Erde*, 1897) and DIELS (*Natürliche Pflanzenfamilien*, 1899-1902), and is now generally accepted.

GOEBEL\* has recently published an account of the Vittarieæ, examining in particular the relationships of the genus *Pleurogramma*, included by DIELS and other systematists as a section of the genus *Monogramma*. This account is by no means complete and takes little or no account of a number of important criteria, such as the vascular anatomy and the origin of the sorus, which have proved themselves to be extremely useful when making systematic comparisons. The only other general account of the Vittarieæ of which I am aware is one by BENEDICT,† which, on the writer's statement, deals "almost entirely with the comparative external morphology and venation of the genera and the probable relationships indicated by these characters." Although GOEBEL and BENEDICT, together with other writers who have described features of interest in single species, have given a considerable body of facts with regard to the Vittarieæ, it has been thought worth while to give a connected account of this group in the present memoir; and especially since the conclusions here reached do not agree with those of previous writers. The present account is based on a critical examination of a wide range of species, particular attention being paid to the vascular structure and other points previously neglected. The material for this investigation was kindly handed over to me by Professor F. O. BOWER in 1923, and to him my best thanks are due. The material for the most part was collected in Jamaica by Professor BOWER; the remainder was from the Calcutta Botanic Gardens, kindly sent to this Department by Mr BURKILL. In addition to the above, Herbarium specimens have been used where no preserved material was available, and I am greatly indebted to Professor WRIGHT SMITH for herbarium material of the rare Fern *Hecistopteris pumila*.

A detailed description of the various genera will now be given, after which the general affinities of the group will be discussed, together with certain stelar problems which are raised by the anatomical construction of the forms examined.

#### VITTARIA, J. E. Smith (1793).

The genus *Vittaria*, along with *Prosaptia* (= *Davallia*), formed the Tribe VII, Vittariaceæ of PRESL. J. SMITH included *Vittaria* together with *Pteropsis* (= *V. angustifolia*) and *Dictyoxiphium* in his Tribe X, Vittarieæ. HOOKER (*Syn. Fil.*) placed it between *Antrophyum* and *Tænitis*, and divided the genus into two sections, § *Euvittaria*, Hk. and §§ *Tæniopsis*, J. Sm., the former having the "sori sunk in a two-lipped marginal groove," and the latter with the "sori in a slightly intramarginal line, with the unaltered edge of the frond produced beyond and often rolled over it." This subdivision is accepted by CHRIST and DIELS in their classification of the genus. In HOOKER's arrangement the § *Euvittaria* contains only a single species, *V. elongata*, whereas §§ *Tæniopsis* has a comparatively large number of ill-defined species differing only in detail from one another. HOOKER gives only eight species with the remark that "the species are very difficult of discrimination, and we have admitted here considerably fewer than M. Fée." CHRISTENSEN, on the other hand, includes over forty species.

BENEDICT‡ has more recently divided the genus into two sections, which do not coincide with those of HOOKER. These are: *Euvittaria*, which appears to include most of the species

\* GOEBEL, "Vittariaceen und Pleurogrammaceen," *Flora*, 1924.

† BENEDICT, "The Genera of the Fern Tribe, Vittarieæ," *Bull. Torrey Bot. Club*, vol. xxxviii.

‡ BENEDICT, *loc. cit.*, p. 160.



of both of the sections of HOOKER and *Radiovittaria*, which contains a small number of species previously included in §§ *Tæniopsis* of HOOKER. The same writer \* has recently described the external morphology and a few points in the anatomy of the species of the latter section, the type species of which is *V. remota*, Fée. Whereas all the species in BENEDICT's section *Euvittaria* have dorsiventral rhizomes and distichous phyllotaxy, the species in the section *Radiovittaria* are stated to have radial stems and polystichous phyllotaxy.

The following account is based on species from both of HOOKER's sections, but, unfortunately, I have not, as yet, had an opportunity of examining any species belonging to BENEDICT's new subgenus *Radiovittaria*.

*Vittaria lineata* (L.), J. Smith.

*Vittaria lineata* (Plate I, A) has a wide distribution in the tropics and subtropics of both hemispheres. The creeping rhizome bears the long, linear fronds in two ranks on its dorsal surface. The fronds are stated to be pendulous, so that the plants look like "bunches of grass."

Together with a number of similar species, *V. lineata* was originally described by J. SMITH under the separate genus *Tæniopsis*, but this latter genus was subsequently given up and reunited by the same writer with *Vittaria*. The name *Tæniopsis* is retained by HOOKER (*Syn. Fil.*) as a sectional name, and *V. lineata* may be taken as a typical example of this section. The material on which the following account is based was collected at Hollymount, Jamaica.

*Anatomy.*—The stele of the mature rhizome is a dorsiventral dictyostele, very similar to the examples of this type of structure described by GWYNNE-VAUGHAN.† Since dorsiventral dictyosteles are frequently present in the rhizomes of the Vittarieæ, a short description of this type of stelar structure may be given here. In the short internodes there is present a single horse-shoe shaped ventral meristele (fig. 1, A; fig. 2, A and B). The xylem is here in the form of a band about two tracheids in thickness and completely surrounded by a sheath of conjunctive parenchyma. Both internal and external phloem are present as a single, or in places double, layer of small, protophloem-like elements, the walls of which stain deeply with hæmatoxylin. External to the phloem there is a well-marked pericycle of large elements, and surrounding the entire meristele is an endodermis. This latter, it may be noted, is in the primary condition and shows a clearly defined Casparian strip.

The method of leaf-trace departure (fig. 1, A–F) is as follows. As the node is approached a small meristele becomes detached from one of the arms of the horse-shoe and moves across to the other arm. The leaf-trace then becomes separated from the axial stele as two strap-shaped strands, one from each side of the leaf-gap. This type of stelar structure, as GWYNNE-VAUGHAN has pointed out, is not far removed from solenostely and results from the fact that the leaf-gaps only overlap very slightly.

The rhizomes occasionally branch in a dichotomous manner, and there is in such examples an equal division of the vascular tissue, each arm having a structure similar to that described above.

*The Frond.*—The linear fronds attain a length of 18 inches and a breadth of  $\frac{3}{8}$  inch. There is a distinct mid-rib, and on either side of it there is a single line of much elongated, almost rectangular areolæ. The venation of the fronds of young plants has been described and figured by BRITTON and TAYLOR, the stages passed through resembling those figured for *Antrophyum* species and *Anetium* (figs. 20 and 30). The first-formed fronds have a single

\* BENEDICT, "A Revision of the Genus *Vittaria*," *Bull. Torrey Bot. Club*, xli, 1914.

† GWYNNE-VAUGHAN, "Observations on the Anatomy of Solenostelic Ferns, Part II," *Ann. Bot.*, vol. xvii.

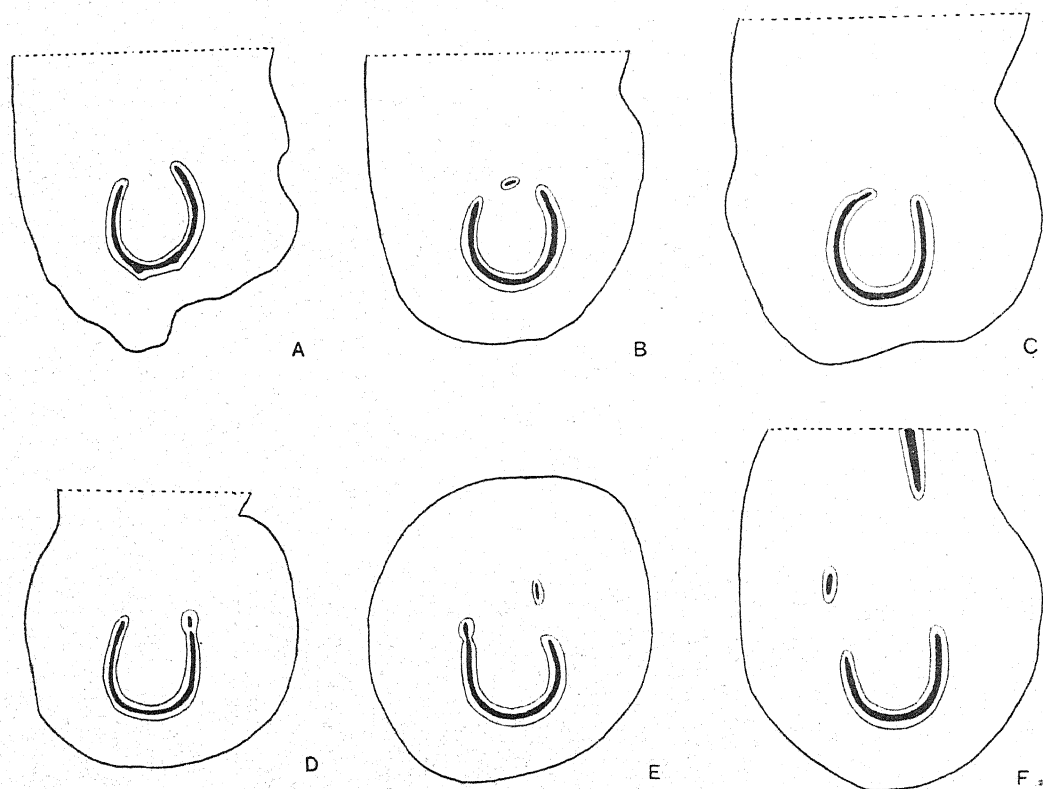


FIG. 1.—*Vittaria lineata*. A-F, series of transverse sections of mature rhizome in succession from below upwards. ( $\times 14$ .)

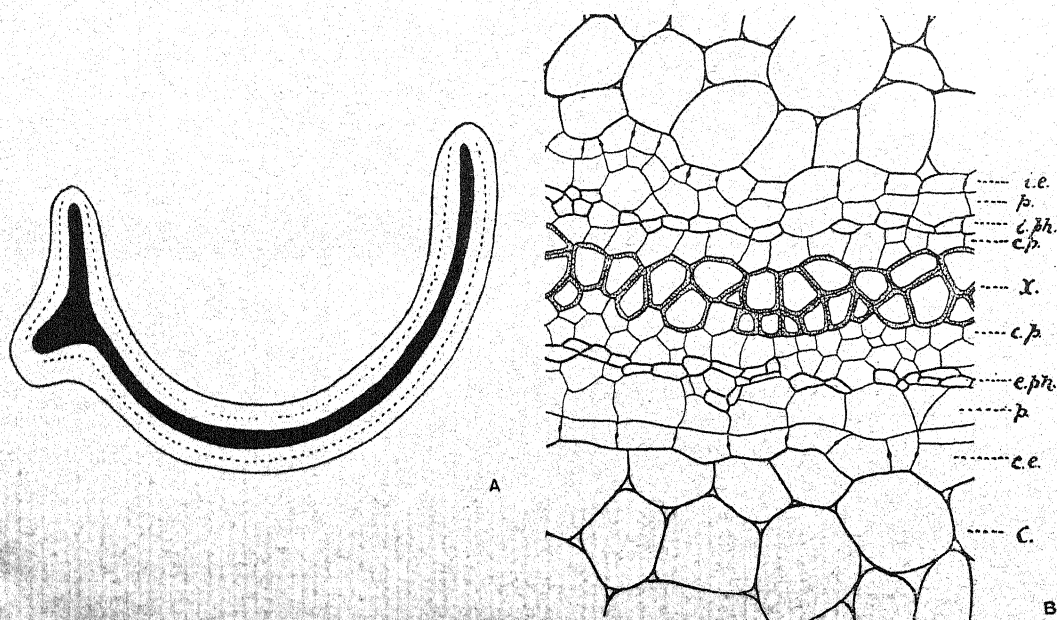


FIG. 2.—*Vittaria lineata*. A, diagram of ventral meristele; xylem black, phloem dotted, endodermis plain line ( $\times 55$ ). B, portion of ventral meristele ( $\times 265$ ): i.e., internal endodermis; p., pericycle; i.ph., internal phloem; c.p., conjunctive parenchyma; x., xylem; e.ph., external phloem; e.e., external endodermis; c., cortex.

vein. The next stage shows a single mesh, and subsequent stages show the establishment of the reticulate venation characteristic of the fronds of mature plants.

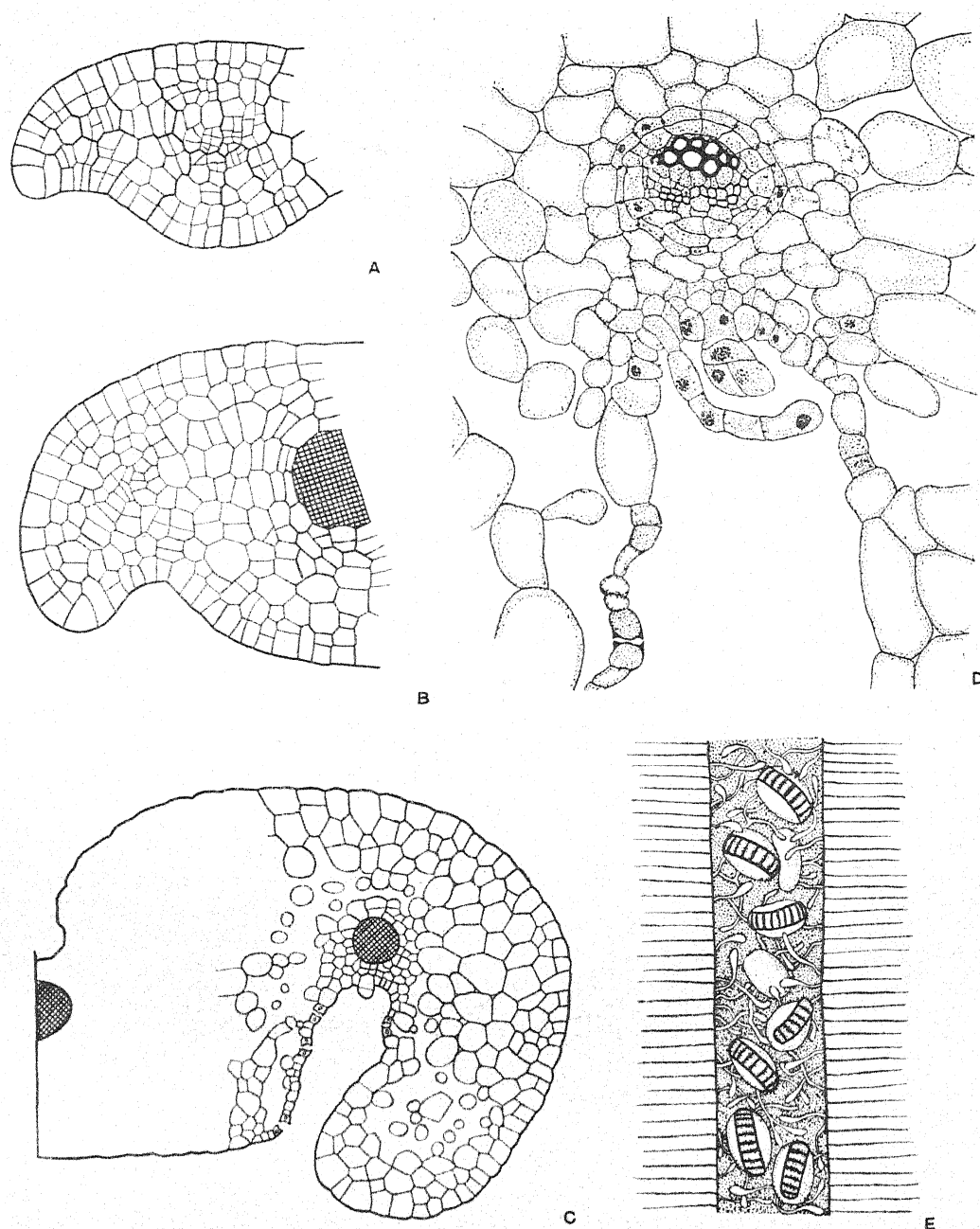


FIG. 3.—*Vittaria lineata*. A-C, vertical sections of successively older sori ( $\times 100$ ). D, portion of sporangial groove showing young sporangium, paraphysis and stomata ( $\times 265$ ). E, sporangial groove in surface view ( $\times 55$ ).

At the base of the petiole of the fronds of mature plants there are two strap-shaped strands of the *Adiantum* type. These divide dichotomously at a higher level, and the two inner shanks unite to form the mid-rib which traverses the length of the frond. Spicule cells are present in the epidermis of the laminal portion. The stomata are mostly confined to the sides of the sporangial grooves, and, on the epidermis lining the latter, simple glandular hairs are present.

*Dermal Appendages*.—The surface of the rhizome and leaf-bases is clothed with clathrate



scales of very characteristic structure, which holds with small, but from the taxonomic point of view important, variations throughout the genus.\* The characteristic appearance of this type of scale is due to the localisation of the thickening to the anticlinal walls, the superficial walls remaining thin and transparent. This differential thickening gives a lattice-like appearance to the whole scale.

*Sporangia*.—The sporangia are borne in two deep grooves over the marginal commissural veins. The arrangement of the sporangia is very irregular, but they are so placed that the

annulus of each is able to function without interference from neighbouring sporangia (fig. 3, E). Intermingled with the sporangia are very numerous paraphyses with club-shaped end cells (fig. 4, B). These paraphyses apparently serve to protect the sporangia in the earlier stages of their development (fig. 3, D), but it is not known whether they have any function at a later stage. The development of the sorus is indicated in fig. 3, A–C, which are from unpublished drawings kindly handed over to me by Professor BOWER. They show very clearly that the origin of the sorus is intramarginal, the true margin of the leaf forming the outer flange of the sporangial groove. The development of the sporangia appears to follow the

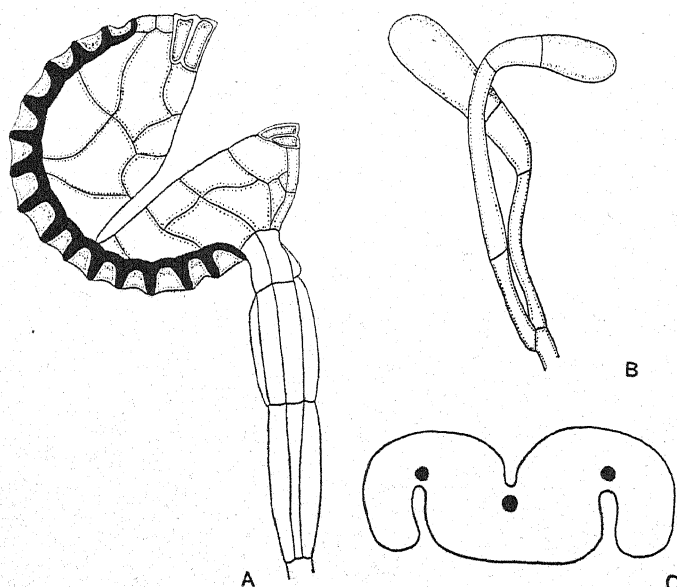


FIG. 4.—*Vittaria lineata*. A, sporangium ( $\times 200$ ). B, paraphysis ( $\times 200$ ). C, transverse section of mature frond ( $\times 20$ ).

usual course characteristic of the higher Leptosporangiate Ferns. The sporangia (fig. 4, A) are marked by a number of features which are common to all the forms of the Vittarieæ examined by me. The capsule has a vertical annulus of fifteen or more cells. The stomium is four-celled and the epi- and hypo-stomium each consist of two cells. The spores are reniform in shape and have a smooth surface. Spore counts yielded the numbers 52 and 61, indicating that the typical number for each sporangium is probably 64. The stalk of the sporangium is peculiar; it is single-celled at its base, but a little below the capsule it consists of several cells. The curious nature of the stalk has a definite relation to the dehiscence of the sporangium, which has been studied in living material by BRITTON and TAYLOR. They state that "As the sporangium ripens all the cells of the upper part of the pedicel become inflated and throw the sporangium back, so that when the split occurs, and the lip cells open by the everting of the annulus, the spores have a less interrupted access to the opening of the groove, their original position being such that did they keep it during the discharge of the spores many of them would become entangled among the branches of paraphyses from which they would be powerless to escape."

#### *Vittaria elongata*, Sw.

*V. elongata* (Plate I, B) is the only species included in the section *Euvittaria* by HOOKER (*Syn. Fil.*). In general habit it closely resembles *V. lineata*, but it appears to be confined to

\* See BENEDICT, "A Revision of the Genus *Vittaria*, J. E. Smith," *Bull. Torrey Bot. Club*, vol. xli, and the older, but apparently less reliable, statements of MÜLLER, *Bot. Zeit.*, 1854.

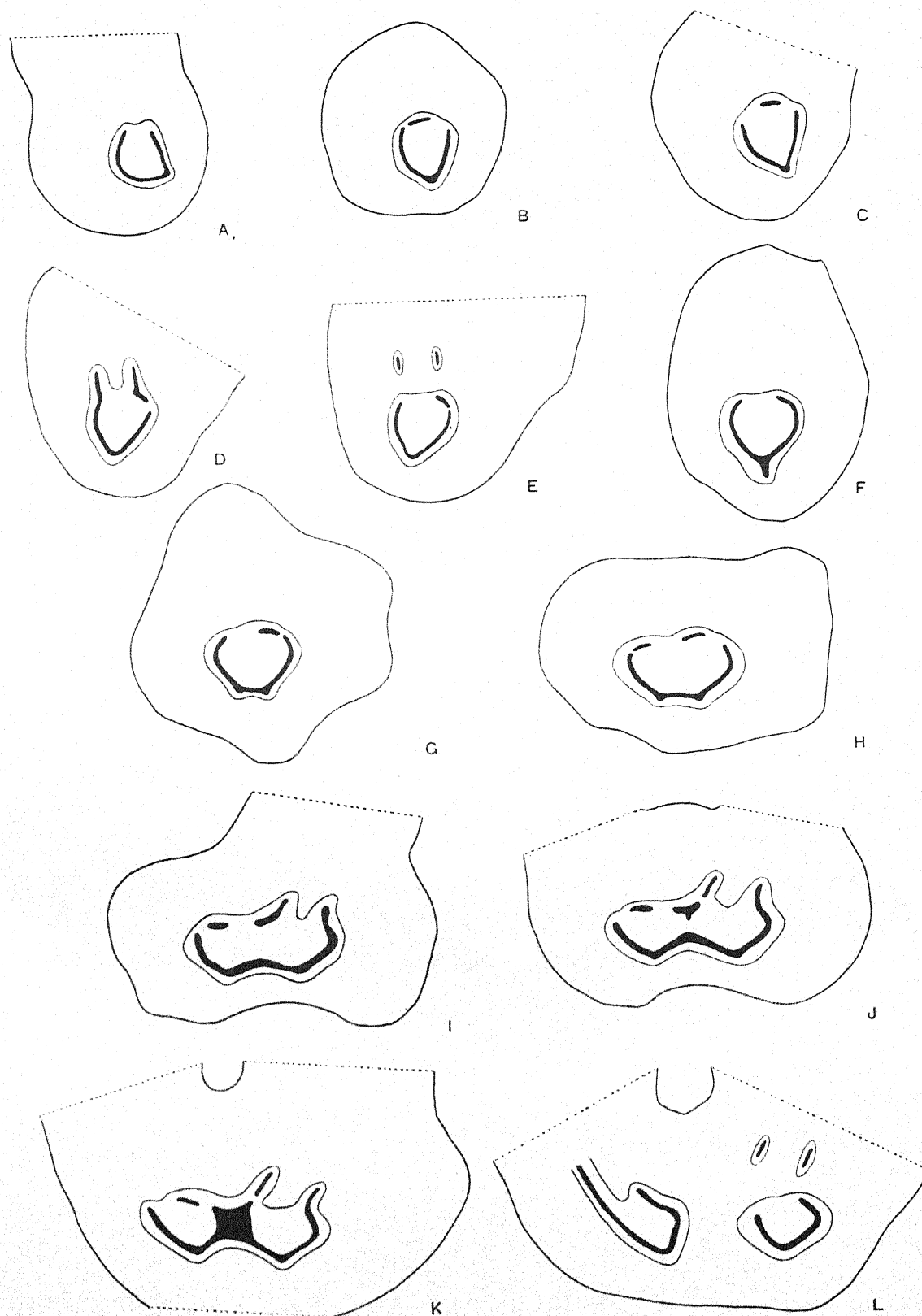


FIG. 5.—*Vittaria elongata*. A-L, series of transverse sections in order from below upwards, showing departure of leaf-traces and a dichotomy of the rhizome. ( $\times 14$ .)

the Eastern Tropics. The material upon which the following account is based was obtained from the Botanic Gardens of Calcutta in 1915.

*Anatomy.*—In the internode of the mature rhizome the stele appears as a more or less cylindrical structure (fig. 5, A). The xylem is in the form of a U-shaped curve, two or three tracheids in thickness, with the opening of the curve facing the dorsal side of the rhizome. Phloem is present both internally and externally as a layer of small elements. Surrounding the stele is an endodermis composed of relatively small elements showing a well-defined Casparian strip. No internal endodermis is present,\* and the centre of the stele is occupied by parenchyma. A several-layered pericycle is present on the outside of the external phloem,

but is not always distinguishable opposite the xylemic gap.

As the node is approached a strand of xylem becomes detached from one arm of the U-curve and moves across, inside the stele, to the other arm (fig. 6). Two strands, each surrounded by an endodermis, then become abstracted from the axial stele, and pass through the cortex into the base of the petiole (fig. 5, B-E). Nowhere during the departure of the leaf-trace does the cortex become continuous with the medulla, the endodermis remaining unbroken throughout. Branching of the rhizome frequently occurs. The branching is dichotomous and does not appear to be related in any way to the insertion of the

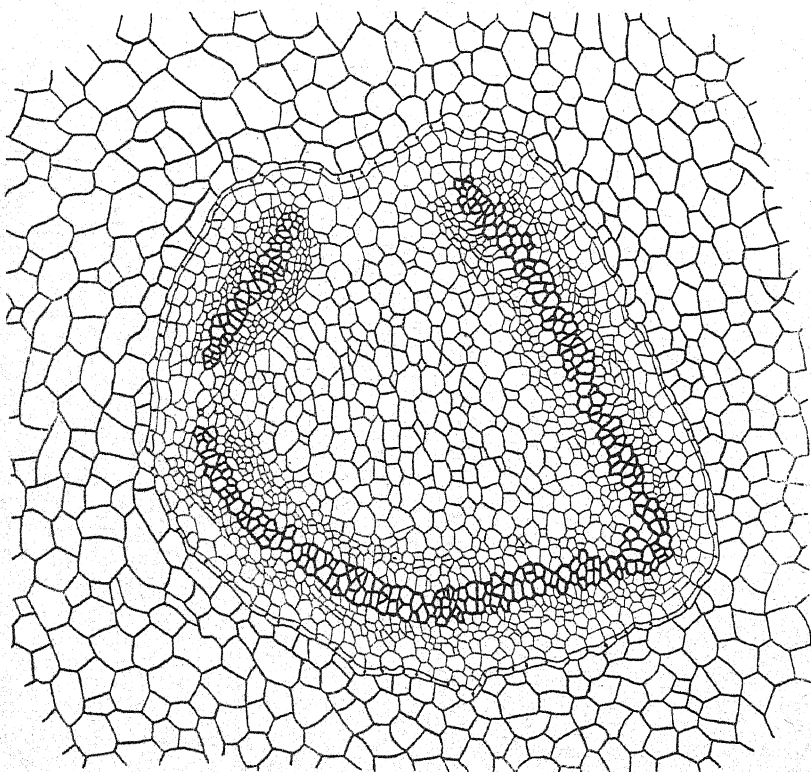


FIG. 6.—The stele of *Vittaria elongata* at the level of B in fig. 5. ( $\times 75$ .)

leaves. The details of one such branching are shown in fig. 5, F-L. In this particular example a leaf is given off from each branch immediately after the bifurcation has taken place, and the changes leading up to the departure of these leaf-traces are initiated before the actual branching occurs. As a result of the changes in the conformation of the stele leading up to the branching, each shank is supplied with a stele essentially similar to the parent one. At no level of the branching is there a gap in the endodermis.

*The Frond.*—The fronds resemble those of *V. lineata* in general appearance, though in the specimens available for examination they are considerably broader. The venation of a sterile frond is indicated in fig. 7, F. Spicule cells are present in the epidermis.

*Dermal Appendages.*—The surface of the rhizomes and leaf-bases is covered with clathrate scales very similar to those of *V. lineata*.

\* JEFFERY (Trans. Roy. Soc. London, B, vol. cxv, p. 132) states that there was an internal endodermis in material from Buitenzorg. This was not the case in any of the material examined by me. GWYNNE-VAUGHAN (*loc. cit.*, p. 719) has also briefly described the anatomy of this species. Some of his specimens agreed with the above description; others he found to be typically dictyostelic, but he remarks that "it is quite possible that some of the specimens examined were wrongly named."



*Sori and Sporangia.*—*V. elongata* (together with *V. Sikkimensis* and *sulcata* according to CHRIST) is characterised by the fact that the sporangia are situated in a marginal groove. It was unfortunately impossible to determine whether the origin of the sorus is truly marginal or not. In the youngest fronds available for examination the sporangial groove is already clearly defined, and it is impossible to determine the origin of the two flanges of the groove. It seems possible from comparison with *V. lineata* that the outer flange is formed by the true margin of the leaf, and that the origin of the sorus is therefore slightly intramarginal. As the frond matures the sporangial groove widens somewhat and the sporangia arise at its base in a "mixed" condition. The sporangia (fig. 7, A) are associated with branched paraphyses, the end cells of which have a very curious and characteristic shape (fig. 7, B). The annulus is generally vertical, though in some examples it appears to extend a little beyond the stalk. The stomium is composed of four cells somewhat narrower than those of *V. lineata*, and there is an epi- and hypo-stomium each consisting of two or three cells. The stalk of the sporangium is single-celled at its base, but, as in the sporangia of *V. lineata*, it becomes several-celled immediately below the capsule. It appears probable that the dilation of the cells below the capsule in this species, as in *V. lineata*, will throw back the mature capsule in such a way that the dispersal of the spores will be rendered more effectual than would otherwise be the case. The spores themselves are reniform and spore counts yielded the numbers 54, 58, 59, and 60, indicating that the typical number for each sporangium is probably 64.

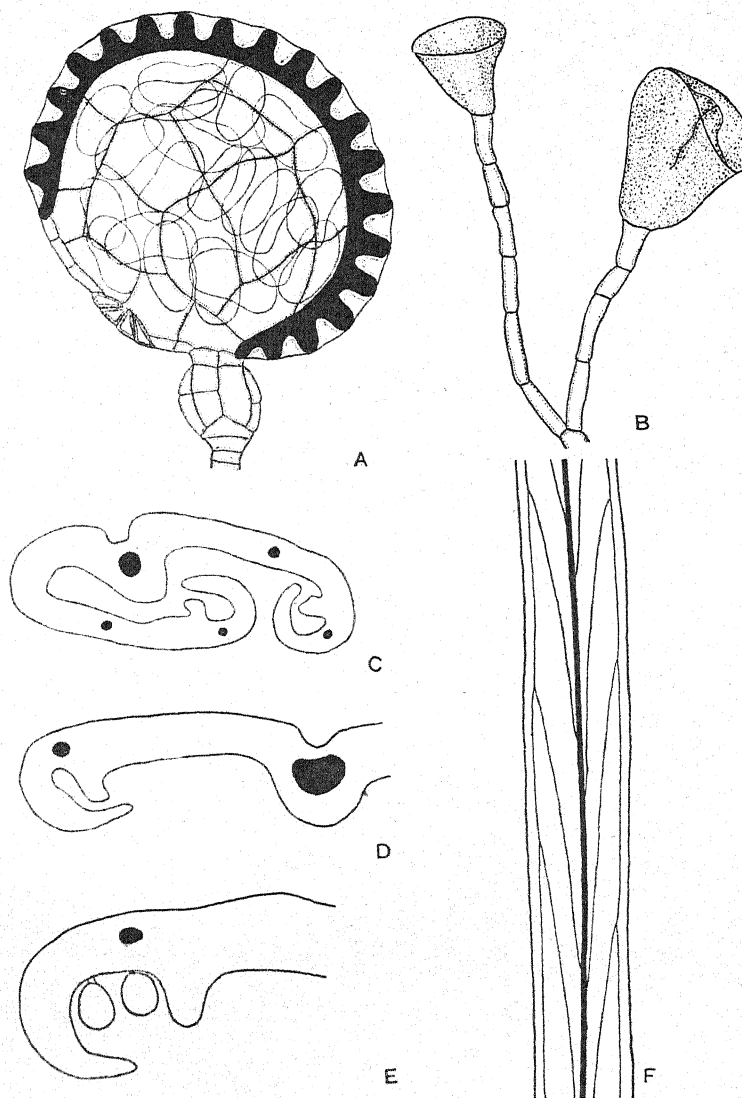


FIG. 7.—*Vittaria elongata*. A, sporangium. B, paraphysis ( $\times 200$ ). C–E, vertical sections of successively older sori ( $\times 22$ ). F, venation of sterile frond ( $\times 2$ ).

*Vittaria angustifolia* (Sw.), Bak.

(= *Pteropsis angustifolia* (Sw.), Desv.)

The habitat of *V. angustifolia* is stated by CHRIST to be from the Antilles to South Brazil. It is a form which is intermediate in many of its characters between *Vittaria* and *Antrophyum*. This intermediate character is seen most strikingly in its venation and soral arrangement.

There are several lines of areolæ on either side of the mid-rib—a condition similar to that present in *Antrophyum*; and, on the other hand, the sporangia are arranged in two definite, slightly intramarginal lines as in *Vittaria*. This combination of characters has resulted in this form having a very varied systematic history. It was originally described by O. SWARTZ in 1788 as *Pteris angustifolia*. Since then it has been placed in a number of different genera by various systematists. DESVAUX (*Prod. de la famille des Fougères*, 1827) and PRESL (*Tentamen*, 1836) described it along with other species under *Pteropsis*. In 1827 SPRENGEL included it in the genus *Tænitis*, and HOOKER did the same in the *Synopsis Filicum* (1868). J. SMITH (*Hist. Fil.*, 1875) retained *Pteropsis*, Desv. for the single species *P. angustifolia*, and this arrangement has been followed by CHRIST (*Die Farnkräuter der Erde*). BENEDICT (*loc. cit.*) also retains this form as a separate genus, *Ananthacorus*, Underwood and Maxon, a generic name which does not appear to have been generally accepted. CHRISTENSEN and DIELS have, however, included it in the genus *Vittaria*, the latter writer making a separate section for it, viz. Section III, *Pteropsis*, and it is the opinion of the present writer that this last arrangement is probably the best one,

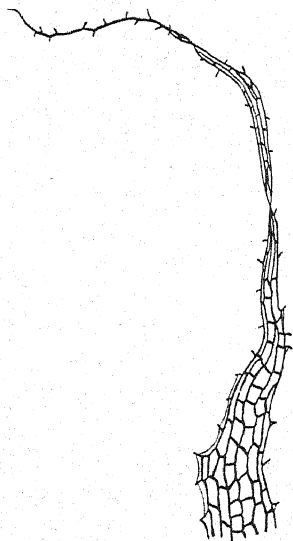


FIG. 8.—Clathrate scale of *Vittaria angustifolia*. ( $\times 22$ .)

having regard to the facts which will now be described. The description is based on a specimen collected by R. H. SCHOMBURGK in British Guiana in 1837.

**Anatomy.**—The mature rhizome has a typical dorsiventral dictyostele. In the internode there is a single U-shaped meristele, the xylem of which forms a narrow band one or two tracheids in thickness. Both internal and external phloem are present as a practically complete band of small, protophloem-like elements. The endodermis is in the primary condition, and the pericycle consists of a single or double row of relatively large elements. The method of leaf-trace departure is indicated in fig. 9, A–D; it is similar in all essentials to that described for *V. lineata*.

**The Frond.**—The fronds, which are 12–18 inches long and about half an inch broad, are inserted somewhat irregularly in two rows on the creeping rhizome. The laminal portion shows a very distinct mid-rib, and on either side of it there are three or four rows of elongated hexagonal meshes (fig. 9, E), thereby differing very markedly from all other *Vittaria* species. There are no points of particular interest in the structure of the lamina except that spicule cells of large size are present in the epidermis (fig. 9, G).

**Dermal Appendages.**—The rhizomes and bases of the petioles are covered by clathrate scales (fig. 8). These approximate in their structure much more nearly to those of *Vittaria* than to those of *Antrophyum*, the rhizoid-like structures, so characteristic of the latter, being entirely absent.

**Sori and Sporangia.**—The sori form almost continuous lines in a submarginal position (fig. 9, E). The sporangia are inserted in a broad groove over the marginal vein, although the groove may extend over the whole of the marginal areola where the latter is small. Intermingled with the sporangia are numerous paraphyses with club-shaped end cells (fig. 9, F). The sporangia are very similar to those of the other *Vittaria* species examined. The material did not permit of any spore counts being made.

## MONOGRAMMA, Schkuhr.

The limits of the genus *Monogramma*, which was founded by SCHKUHR in 1799, have varied considerably in the hands of different systematists. HOOKER divided the genus into two sections: § *Eumonogramme*, having the "frond with central vein only,"\* and §§ *Pleuro-*

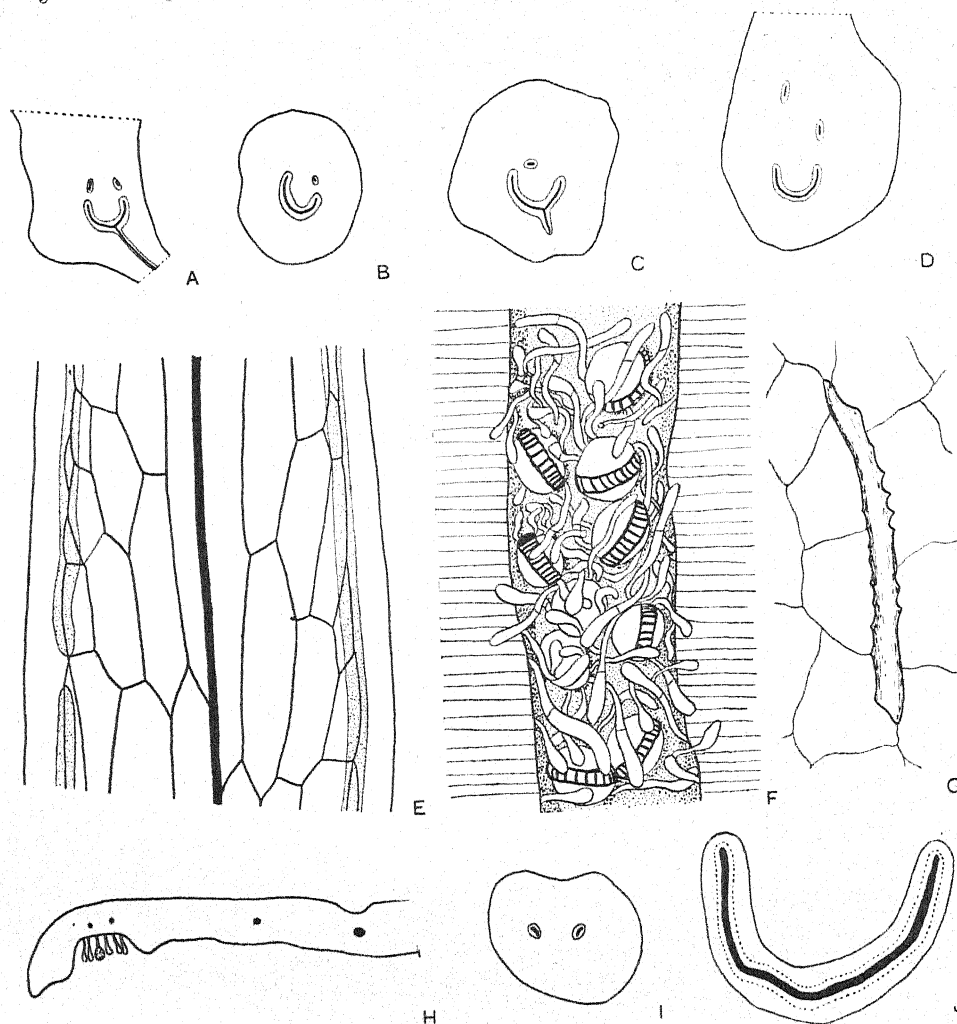


FIG. 9.—*Vittaria angustifolia*. A-D, series of transverse sections of mature rhizome in order from below upwards ( $\times 14$ ). E, venation of fertile frond ( $\times 4$ ). F, sporangial groove in surface view ( $\times 42$ ). G, spicule cell ( $\times 200$ ). H, transverse section of frond in fertile region ( $\times 14$ ). I, transverse section of petiole ( $\times 14$ ). J, diagram of ventral meristele ( $\times 65$ ).

*gramme*, having "fronds with indistinct simple lateral veins in addition to the mid-rib." In 1893 POIRAULT† pointed out that spicule cells were absent from the fronds of one or two of the species in the *Pleurogramme* section, and in 1911 BENEDICT made the general statement that the species in the section *Pleurogramme* were so unlike those of the section *Eumonogramme* that they would be better separated as a distinct genus. GOEBEL (*loc. cit.*, 1924) has recently emphasised this point, demonstrating that the *Pleurogramme* types possess no spicule cells,

\* This diagnosis is incorrect since there are lateral veins in a number of the species included under *Eumonogramme*. This inaccuracy is probably due to the difficulty with which the venation is made out in such extremely narrow fronds. It only appears clearly after treatment of the frond with Eau de Javelle and staining with safranin or, better still, with ammoniacal fuchsin.

† POIRAULT, *Ann. des Sc. Nat.*, 1893, p. 208.



have sporangia with a two-celled stomium, possess sclerenchyma in their rhizomes, and that clathrate scales are absent from their rhizomes and leaf-bases. It is clear therefore that BENEDICT was correct in stating that "there is ample evidence to show that they are not only not to be included in *Monogramma*, but they may not even be retained in the tribe Vittarieæ." *Pleurogramma* must, then, be reinstated as a substantive genus (with affinities elsewhere than with the Vittarieæ) and *Monogramma* limited to the *Eumonogramma* types. This confirms the arrangement of PRESL, who not only recognised the two as separate genera but placed them in different tribes. CHRIST (1897) also recognised the two as separate genera, but he included both of them in the Vittarieæ, a course which does not appear to be justified. GOEBEL (*loc. cit.*, 1924) holds the view that the *Eumonogramma* species would be better separated into two genera, namely, *Monogramma* and *Vaginularia*, Fée. The former genus would contain those species not possessing lateral veins, the latter those possessing lateral veins. Going along with this difference of venation are differences in the detailed structure of the paraphyses and in the type of stomata. These differences appear to be too small to justify generic separation of forms which are almost identical in their anatomical construction, in the structure of their sporangia and in the form of their clathrate scales. Moreover, the species of the *Eumonogramma* section show a gradual transition from forms almost identical with *Vittaria* species to the extreme simplicity of the *M. graminea* type. For the purpose of this memoir, then, the species will be described under the genus *Monogramma*, Schkuhr, this genus being now limited to those forms included by HOOKER and other systematists in the section *Eumonogramme*. The number of species included in this latter section varies considerably in the different systematic works owing to the fact that the delimitation of the species, as in *Vittaria*, is a matter of considerable difficulty. The species which will now be described illustrate, however, the extremes of variation to be found within the genus.

*Monogramma paradoxa* (Fée), Bedd.

(=*M. Junghuhnii*, Hk.)

*M. paradoxa* (Plate I, C) is a relatively small, grass-like plant found in Ceylon, Java, Philippines, and Polynesian Islands. It has a very slender rhizome, on which the fronds are arranged in two rows on the dorsal surface. The fertile leaves possess lateral veins, and on account of this feature GOEBEL places this species in the genus *Vaginularia*, Fée. The following account is based on herbarium specimens collected by LOBB in Java.

*Anatomy.*—The anatomy of the rhizome is very similar to that of *M. graminea*, and as the material of the latter species was more suitable for examination the detailed description of the anatomy will be given for that species. It may be briefly stated that the stele is protostelic with a V-shaped xylem mass, and that the leaf-traces depart as single strands from the two arms of the V-shaped mass alternately. As in *M. graminea*, an equal dichotomy of the axis sometimes occurs. The structure of the root is very simple, the small stele possessing only three or four tracheids.

*The Frond.*—The fronds of the specimens available for examination were 12–15 cm. long. In the lower sterile portion of the lamina only the mid-rib is present, but in the fertile region there is a single lateral vein which runs parallel to the mid-rib for a considerable distance and then, after converging towards the mid-rib, dies out without actually coming into contact with the latter (fig. 10, G). In small sterile specimens examined by BENEDICT the lateral vein is shown as uniting with the mid-rib and so forming a single areola (fig. 10, A). In larger fertile specimens examined by the same writer the fronds reach a length of 25 cm.

and show two areolæ in the broadest portion of their lamina (fig. 10, B). This more complex venation approximates to that characteristic of *Vittaria*, and, indeed, presents an intermediate condition between the latter and the extremely simple venation of such forms as *M. graminea*.

Spicule cells of great length are present in abundance in the epidermis.

*Dermal Appendages*.—The clathrate scales (fig. 10, H) are very similar to those of *Vittaria* species.

*Sporangia*.—In the specimens examined the sporangia are borne in a single groove which extends the whole length of the lateral vein. In the larger specimens figured by BENEDICT, and in the specimens figured by HOOKER, the sporangial groove is double in the broadest portion of the frond, becoming single in the narrower distal region. The morphology of the sporangial grooves and the ridges bounding them has been discussed at length by GOEBEL (*loc. cit.*, 1924), but no satisfactory conclusion can be reached until the ontogenetic development of the fronds has been traced. The double-groove condition appears, however, to be comparable with such a form as *V. lineata*, and the single-groove condition may possibly be regarded as a reduction from this.

The sporangia (fig. 10, E) are of the usual Vittariaceous type, with an annulus of 15–18 cells and a four-celled stomium. The sporangial stalk is single-celled below, but immediately beneath the capsule it is several-celled, as in the sporangia of *Vittaria* species. The paraphyses (fig. 10, F) which are intermingled with the sporangia are of a very simple type and differ from those of most other Vittarieæ in not having club-shaped end cells.

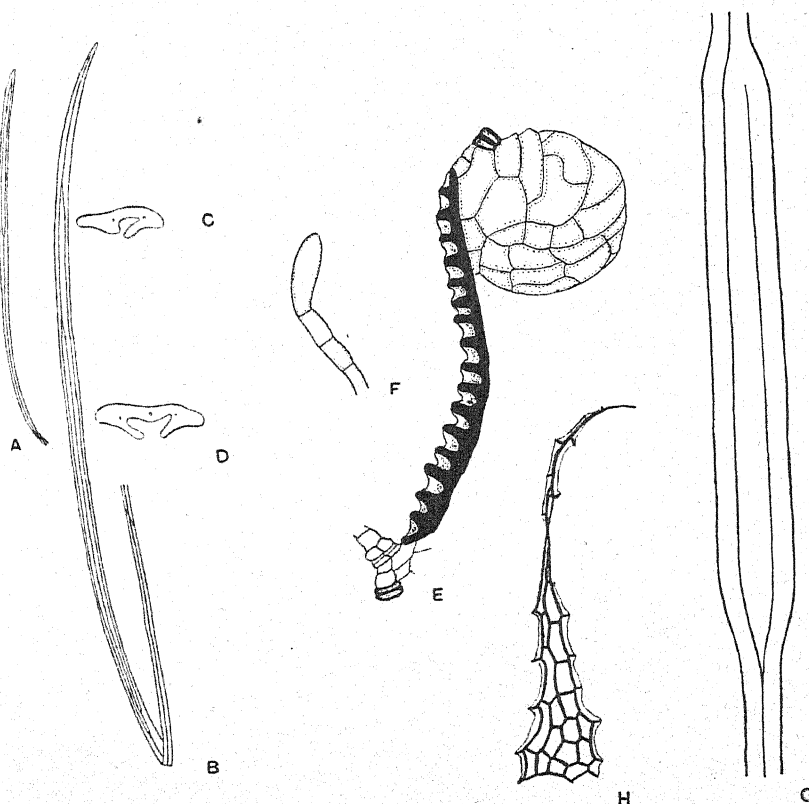


FIG. 10.—*Monogramma paradoxa*. A, sterile frond. B, fertile frond. C and D, sections of fertile frond at levels indicated (A–D after Benedict). E, sporangium ( $\times 135$ ). F, paraphysis ( $\times 135$ ). G, diagram of venation in fertile region. H, clathrate scale ( $\times 44$ ).

#### *Monogramma trichoidea*, J. Sm.

This species from the Philippines and Borneo is a very small one, with an extremely slender rhizome and thread-like fronds 3–4 inches long. On account of the presence of lateral veins the species is another of those included by GOEBEL in the genus *Vaginularia*. The following account is based on herbarium specimens collected by CUMING in Luzon, the largest of the Philippine Islands.

*Anatomy*.—The anatomy has been briefly described by GOEBEL (*Organographie*, p. 911),

and I have been able to verify this description. The stele is protostelic and is surrounded by an endodermis in the primary condition. The xylem consists of a horse-shoe curve, one or at most two tracheids in thickness. Phloem is present on both the dorsal and ventral sides of this and there is a well-marked pericycle. The leaf-traces depart alternately from the right and left of the stele as very small and simple strands. Fig. 11, A is a slightly diagrammatised drawing of a dichotomously branched rhizome cleared in Eau de Javelle and stained with ammoniacal fuchsin. An interesting point is that in the older portion of the rhizome there is a definite relationship between the insertion of the roots and leaves, there being one root at each leaf insertion.

*The Frond.*—The sterile fronds have a very simple structure showing an indistinct mid-

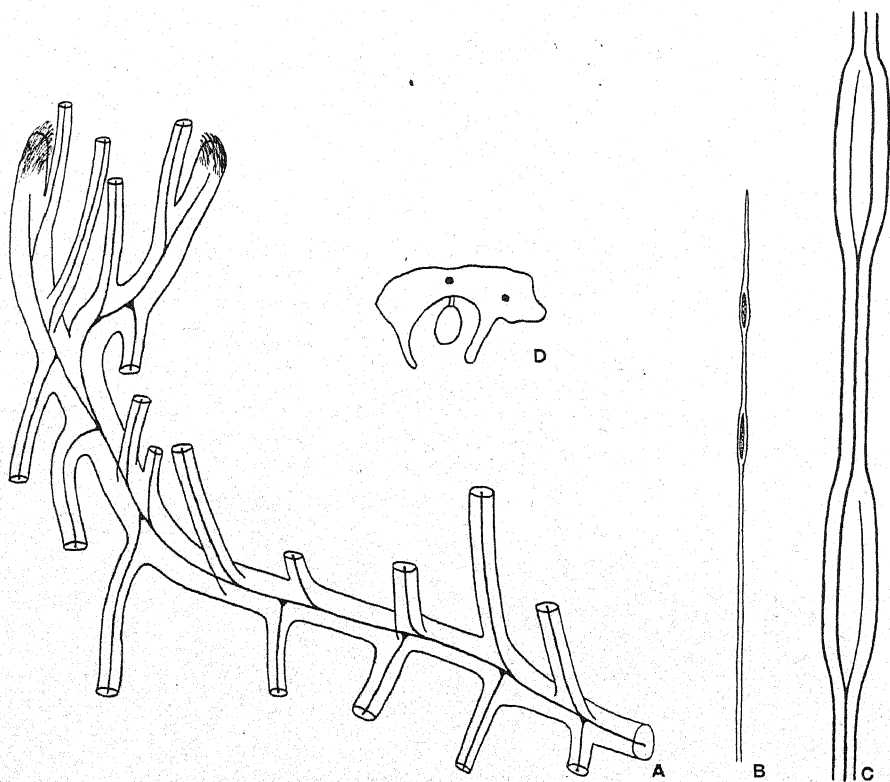


FIG. 11.—*Monogramma trichoidea*. A, rhizome cleared in Eau de Javelle and stained in ammoniacal fuchsin, showing the general course of the vascular strands and a dichotomy of the rhizome ( $\times 14$ ). B, fertile frond. C, venation of sporangiferous regions. D, transverse section of the fertile region of a frond ( $\times 55$ ).

rib and no lateral veins. The fertile fronds (fig. 11, B) show two or three sporangiferous regions, each about  $\frac{1}{4}$  inch long, and in these regions the frond is somewhat dilated. As in the fronds of *M. paradoxa*, the venation is obscure, but after treatment with Eau de Javelle and ammoniacal fuchsin it is possible to make out that in each sporangiferous region there is a lateral vein which runs parallel to the mid-rib (fig. 11, C). GOEBEL states that occasionally the lateral vein joins up with the mid-rib to form a single areola.

Numerous long, spicule cells are present in the epidermis.

*Dermal Appendages.*—The clathrate scales are of exactly the same type as those of *M. paradoxa*.

*Sporangia.*—In each sporangiferous area the sporangia are situated at the base of a broad and deep groove, bounded by two flanges, the morphology of which is obscure in the absence of any data concerning the ontogenetic development (fig. 11, D). The sorus is seated over



the single lateral vein. The sporangia, which are mixed with branched paraphyses, are almost identical with those of *M. paradoxa*.

*Monogramma graminea*, Schkuhr.

*M. graminea* (Plate I, D) is another small form, with fronds about 2 inches long, which

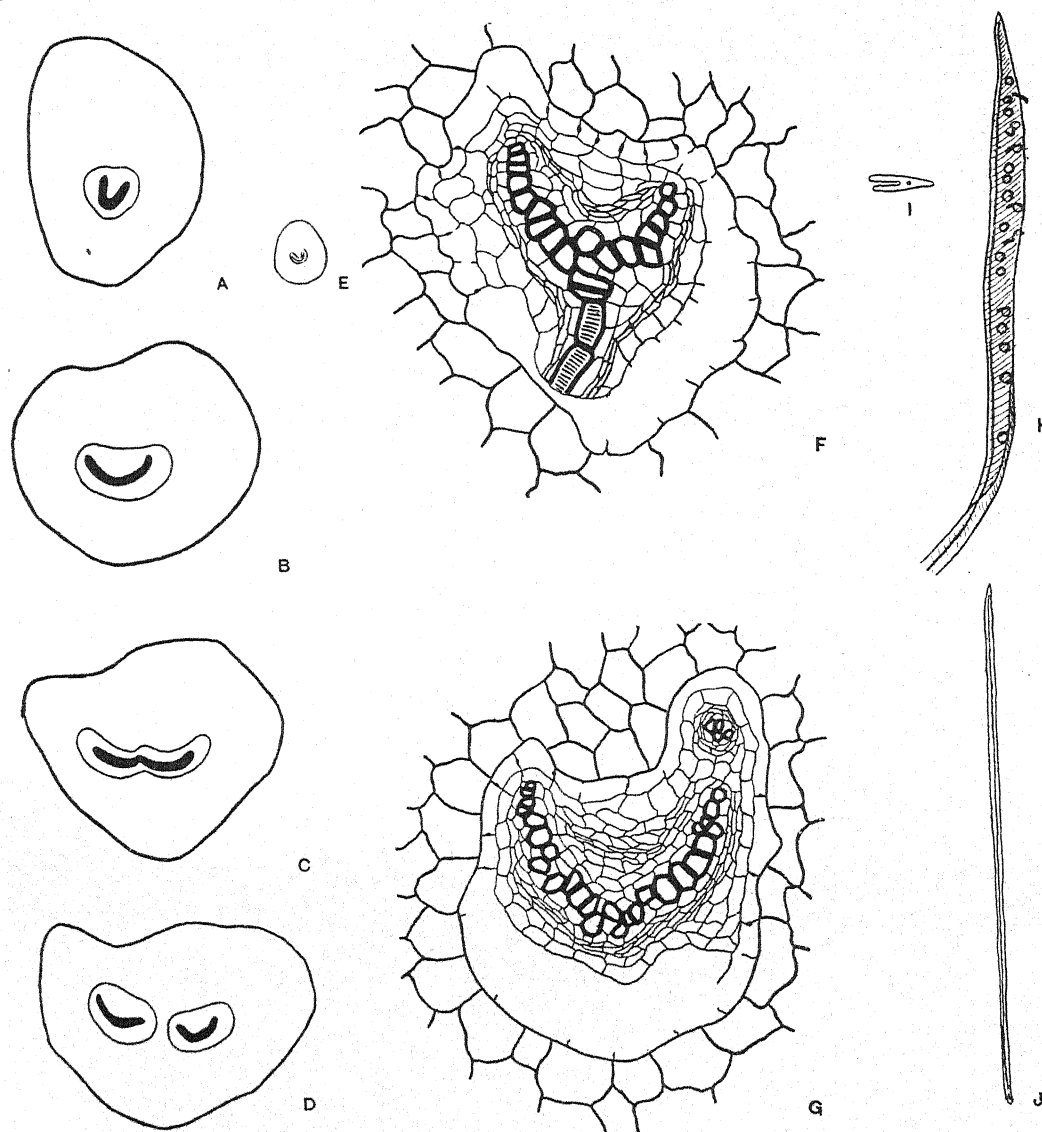


FIG. 12.—*Monogramma graminea*. A-D, series of transverse sections of a mature rhizome in the region of branching ( $\times 55$ ). E, transverse section of rhizome ( $\times 14$ ). F and G, details of stele ( $\times 265$ ). H, fertile region of frond. I, transverse section of frond in fertile region. J, sterile frond.

is found in Cape Colony, Mauritius, and the Reunion Islands. The following account is based on herbarium specimens collected in the last-named habitat.

*Anatomy.*—The stelar construction of the small fleshy rhizome is very simple. In the internodes the stele (fig. 12, F) is a small crescent-shaped structure, the xylem being in the form of a horse-shoe curve of twelve to eighteen tracheids. The xylem is surrounded in turn by a parenchymatous sheath, phloem, a pericycle, and endodermis, this latter being in the primary condition. The phloem, as in *Vittaria*, is composed of small protophloem-like elements.

As the node is approached one arm of the xylem curve becomes elongated, and finally a small group of three or four tracheids, surrounded by a small amount of phloem and an endodermis, is abstracted off from the axial stele and passes out through the cortex into the leaf-base (fig. 12, G). At the next node this process is repeated, and a similar small and simple strand is abstracted off from the other side of the axial stele.

Branching of the rhizome frequently occurs in a typically dichotomous manner. As the level of branching is approached the stele broadens out, the xylem mass becoming very broadly U-shaped. The stele then takes on the double U-shaped conformation shown in fig. 12, C, and finally each arm of the branching is supplied with a strand similar in all respects to the parent axial stele (fig. 12, D).

The root-traces depart from the ventral side of the stele, but their insertion does not appear to be related to the insertion of the leaves.

*The Frond.*—The fronds of *M. graminea* are exceedingly simple. The single strand which passes off from the axial stele remains undivided throughout the length of the linear frond (fig. 12, J), lateral veins being absent in all the specimens examined. Anatomically the frond is very simply constructed and resembles closely that figured for *M. trichoidea* by GOEBEL (*Organ.*, p. 1046). The vascular strand, as seen in section, consists of two or three tracheids surrounded by a small amount of phloem, a conspicuous pericycle, and an endodermis.

*Dermal Appendages.*—The surface of the rhizome is clothed with clathrate scales very similar to those described for *Vittaria* species.

*Sporangia.*—The fertile region of the frond is distal and occupies about half an inch at the apex of certain of the fronds (fig. 12, H). A section across the fertile region shows that the sporangia are seated in a deep groove formed apparently by a folding of the lamina (fig. 12, I). A knowledge of the ontogeny of the fertile frond is required before a correct morphological interpretation of the fertile region can be advanced. The sporangia themselves are very similar to those of *Vittaria* species. They have a similar type of stalk dilated in the distal region. The capsule has an annulus of fifteen to twenty cells; the stomium is four-celled; and there is an epi- and hypo-stomium each consisting of two cells. The spores are tetrahedral in form, and spore counts indicate that 32 to 48 spores are formed in each sporangium.

#### ANTROPHYUM, Kaulfuss.

*Antrophyum* is described by HOOKER (*Syn. Fil.*) as "a small genus of closely allied species almost restricted to the tropics, all with simple fronds of firm but fleshy texture and copious uniform hexagonal areolæ." CHRISTENSEN (*Index Fil.*) gives twenty-seven species, but DIELS (*Pflanzenfam.*) and HOOKER only give sixteen species. This discrepancy is accounted for by the fact that the limits of many of the species are not at all clear. The species are divided by both HOOKER and DIELS into two groups according as to whether the sori are sunk in a groove or whether they are superficial or but slightly immersed. BENEDICT has recently removed a number of species of *Antrophyum* into a separate genus *Polytaenium*, Desv., mainly on the basis of differences of venation and geographical distribution. The genus *Antrophyum* is limited by BENEDICT to the Old World species; these are characterised by the fact that the venation is of the "single-net type," i.e. there is no distinct mid-rib, and the areolæ are always directed towards the base of the lamina. On the other hand, the New World species included by BENEDICT in the genus *Polytaenium* have a "double-net type" of venation with a distinct mid-rib, and, as a further point of difference, they possess no paraphyses. It appears doubtful, however, whether these differences are sufficient to warrant a generic separation of the two

types. The anatomical construction, the structure and distribution of the sporangia, and the structure of the clathrate scales are all so similar throughout the genus as delimited by HOOKER, DIELS, and CHRISTENSEN that there seems to be no good reason for reinstating the genus *Polytænium*, Desv.

The following species have been examined: *A. reticulatum*, Kaulf., *plantagineum*, Kaulf., *lineatum*, Kaulf., *lanccolatum*, Kaulf., and *brasilianum*, C. Chr. These include both forms with their sori sunk in a groove and those with superficial sporangia. They also include species placed by BENEDICT in the genus *Polytænium*, Desv.

*Antrophyum reticulatum*, Kaulf.

The general appearance of *A. reticulatum* is shown in Plate II, A. The fronds, which attain a length of 12 inches and a breadth of 1-3 inches, are borne in two irregular rows on the dorsal surface of the comparatively stout creeping rhizome. The species appears to be confined to the Eastern Hemisphere, and HOOKER describes it as occurring in the "Himalayas, Ceylon, and Malaccas to Aneitium and Queensland." The material on which the following account is based was collected in Singapore by Mr BURKILL.

*Anatomy.*—The mature rhizome possesses a dorsiventral dictyostele which differs only slightly from the type described for *Vittaria lineata*. The distribution of the inner phloem is, however, peculiar and shows a divergence from the condition present in a typical example of this type of stelar construction. It is only present in the dorsal regions of the meristele,

being replaced by what GWYNNE-VAUGHAN has termed "pericyclic parenchyma" in the ventral portion of the horse-shoe curve (fig. 13, A and B). A slight variant of the normal dorsiventral

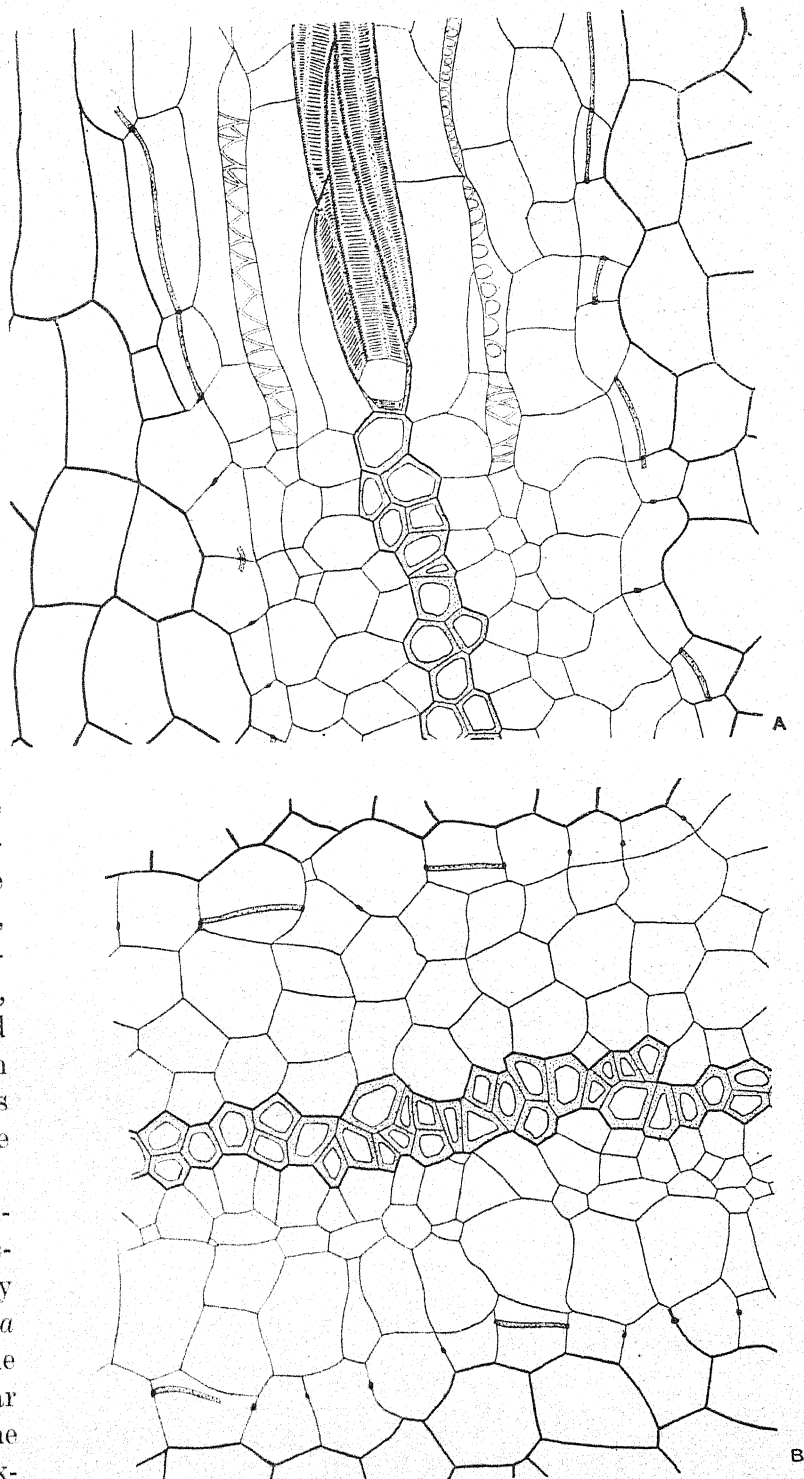


FIG. 13.—*Antrophyum reticulatum*. A, dorsal arm of ventral meristele with leaf-trace shown in longitudinal section. B, ventral portion of meristele. ( $\times 265$ .)



dictyostele is present in some of the rhizomes examined. As far as the stele itself, as delimited by the endodermis, is concerned the leaf-gap is closed before the succeeding leaf-gap is formed, but there is a slight overlapping of the xylic gaps. This results in the appearance of a small dorsal strand of xylem which moves across, within the stele, from one side of the U-shaped

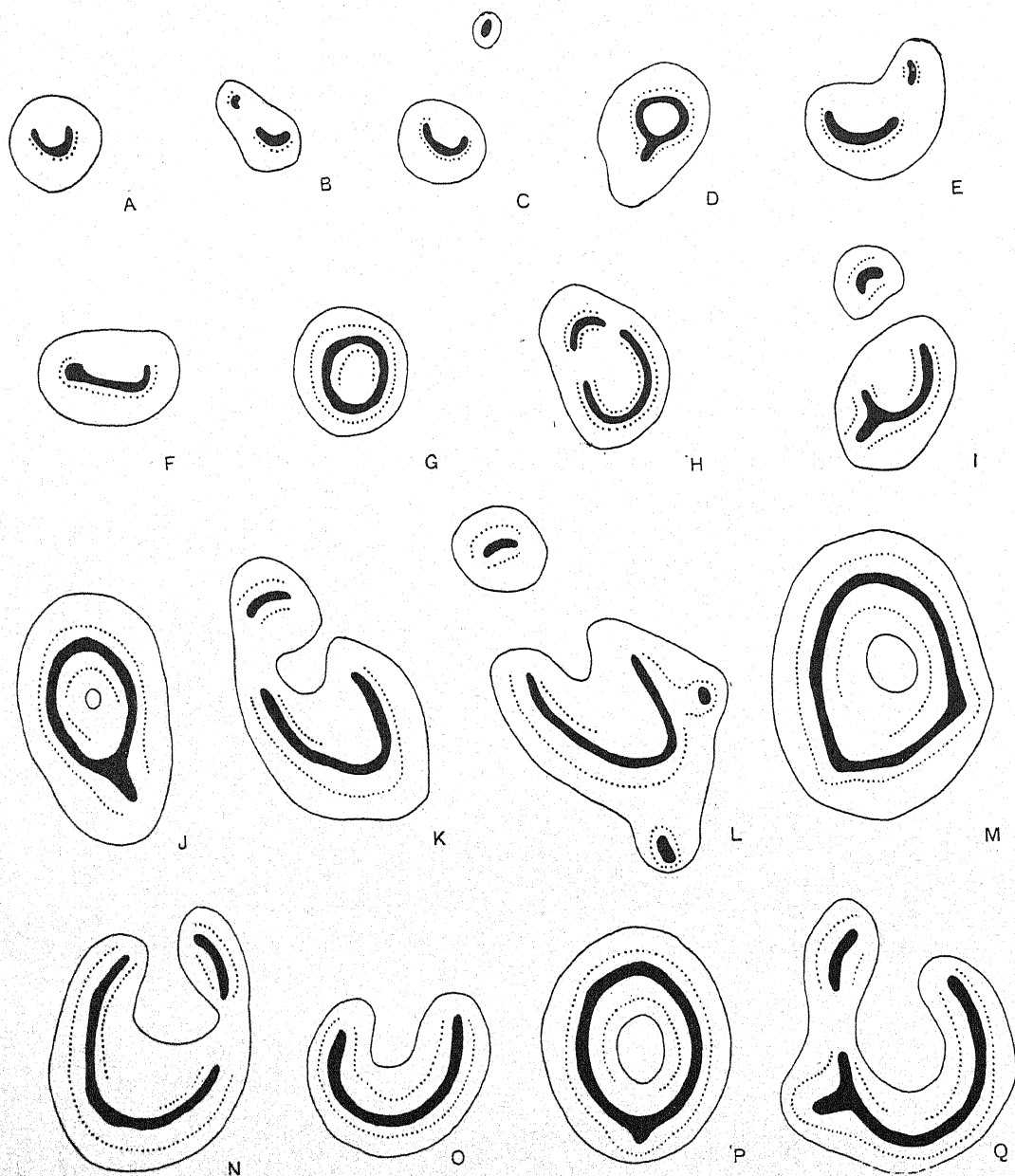


FIG. 14.—*Antrophyum reticulatum*. A-Q, series of successive transverse sections of the stele of the rhizome of a seedling plant in order from below upwards. Description in text. ( $\times 70$ )

curve of xylem to the other at each node. This type of structure is still nearer to solenostely than is the normal dorsiventral dictyostele.

It was possible to trace the ontogenetic stages in the development of the dorsiventral dictyostele above described. In the lowest internode observed (fig. 14, A) the small cylindrical stele has the following structure as seen in transverse section. The xylem mass is in the form of a shallow horse-shoe curve one or two tracheids in thickness. On the ventral side of the xylem, and separated from it by a layer of conjunctive parenchyma, is a layer of phloem

elements, distinguished by their small size and by the fact that their walls stain deeply with hæmatoxylin. No phloem was observed on the dorsal side of the xylem and its place is taken by large-celled parenchyma. The stele is surrounded by a large-celled pericycle and by an endodermis which is in the primary condition; the Casparian strip is distinguishable but is not well developed. As the first node is approached, one arm of the curve of xylem becomes somewhat extended, and finally the first leaf-trace (fig. 14, B, and Plate III, C) is abstricted off as a small group of two or three tracheids and a few phloem elements, surrounded by pericycle and endodermis. There is no break in the endodermis during this process, nor is the axial stele disturbed in any way by the departure of the leaf-trace. The second and third internodes are similar to the first one, and the second and third leaf-traces depart in a very similar manner to the first trace, being abstricted off from the right and left arms of the horse-shoe curve alternately. In the lower portion of the fourth internode the structure is as in the lower internodes, but at higher levels (fig. 14, D) the arms of the xylem curve close round to the dorsal side so that a practically complete ring of xylem is formed. This is surrounded by conjunctive parenchyma, phloem, pericycle, and endodermis. The interior of the ring is occupied by large-celled parenchyma and a few phloem elements. The fourth leaf-trace departs from this stele in the manner indicated in fig. 14, E. The fifth leaf-trace departs in a similar fashion. In the basal region of the sixth internode (fig. 14, F) the stele shows a somewhat flattened curve of xylem with phloem present round the convex side of it. As the internode is traversed the xylem curve closes round to the dorsal surface so that a practically complete ring is formed (fig. 14, G and Plate III, D). At this level there is a ring of external phloem; internal phloem is present on the dorsal side of the stele only, and no internal endodermis is evident. Fig. 14, H and I indicate the way in which the sixth leaf-trace departs as a crescentic strand of xylem with both internal and external phloem. The seventh leaf-trace departs in a very similar manner. As the eighth internode is traversed the xylem again forms a ring, one or two tracheids in thickness and of considerably greater diameter than the xyletic rings observed in the lower internodes. It is surrounded on the outside in centrifugal order by conjunctive parenchyma, a complete ring of phloem, pericycle, and endodermis. Inside the xylem ring are conjunctive parenchyma, a band of phloem in the dorsal and lateral regions, and large-celled parenchyma in the centre. At higher levels, *i.e.* approaching the eighth node, a small circle of internal endodermis makes its appearance, indicating a slight pocketing in of the endodermis at the node (fig. 14, J). The eighth leaf-trace leaves the axial stele in the manner indicated in fig. 14, K and L. The trace has a crescentic xylem mass which is for the most part only one tracheid in thickness; phloem is present on both the ad- and ab-axial surfaces. The ninth, tenth, and eleventh leaf-traces depart in a very similar manner to the eighth, and the only point which need be noted is that the ninth and subsequent leaf-traces divide into two portions during their passage through the cortex so that two strands enter the petioles of these leaves. Internal endodermis makes its appearance low down in the twelfth internode indicating a deep pocketing in of the endodermis at the twelfth node. As a result of this a solenostelic structure is seen in the upper portion of the internode (fig. 14, M). The twelfth leaf-trace leaves in the manner indicated in fig. 14, N, and from this level on to the seventeenth internode a typically solenostelic type of structure is present, the only point of interest being the deficiency of the internal phloem on the ventral side of the stele (fig. 14, P, Q and Plate III, E). The first divergence from normal solenostelic structure was observed in the seventeenth internode. As the node is traversed the sixteenth leaf-gap becomes closed so far as the endodermis is concerned (fig. 15, A) but the xyletic gap remains open. There is here, then, a complete ring of external and internal endo-

dermis; the xylem ring is still showing a gap; and phloem is present both internally and externally with the same limits as the xylem except that it is absent on the internal ventral side. As the node is approached a small group of tracheids, with a small amount of internal and external phloem, becomes separated off from the main xylem curve (fig. 15, A and B). The first indication of the departing seventeenth leaf-trace is here seen as an arc of tissue bulging out somewhat from the circular outline of the stele. At levels approaching the node the small mass of xylem and phloem moves slowly across from one side of the xylem gap to the other, and simultaneously the curve of xylem and phloem forming the leaf-trace becomes

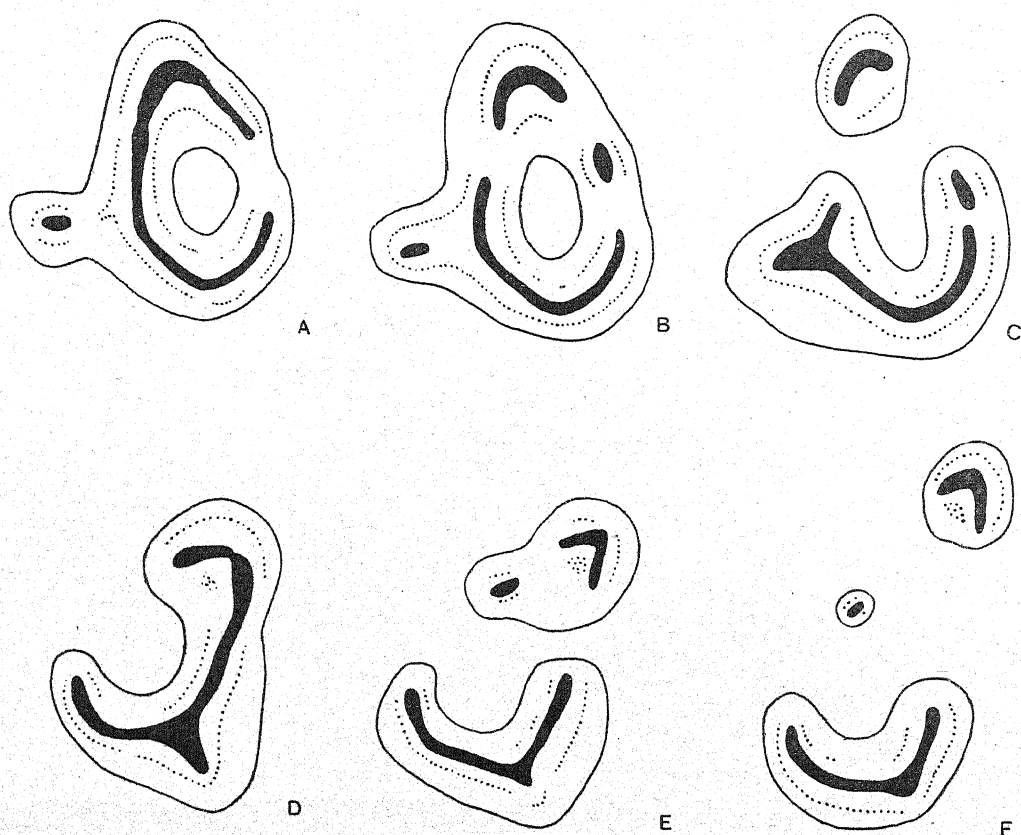


FIG. 15.—*Antrophyum reticulatum*. A-F, Continuation of series in fig. 14. ( $\times 70$ .)

detached from the axial stele (fig. 15, C). It may be noted that this type of structure \* is on the border-line between solenostely and dorsiventral dictyostely. The eighteenth and nineteenth internodes revert to the normal solenostelic structure and show no points of particular interest. At the base of the twentieth internode the stele has the usual horse-shoe form. As the node is approached changes take place in the conformation of the strand as indicated in fig. 15, D, E, and F. The important point is the appearance of a small dorsal meristele which moves across from one side of the leaf-gap to the other surrounded by its own endodermis. This indicates the establishment of a dorsiventral dictyostelic condition similar to that described for the mature rhizome. The twenty-first internode and node revert to the solenostelic condition, but in the twenty-second node there is an indication of dorsiventral dictyostely being again initiated. At this level the strands of the specimen examined are in

\* Cf. the structure described as occurring occasionally in the mature rhizome and the account of GWYNNE-VAUGHAN of the stele of *Cheilanthes lindigera*.



the desmogen condition, and any further steps leading up to the persistent dorsiventral dictyostely of the mature rhizome were not observed.

*Root.*—There is nothing of particular interest in the anatomy of the root, it having the diarch structure typical for the majority of Leptosporangiate Ferns. The roots, like those of all the other Vittariæ, are clothed with a dense mass of dark brown root hairs, so that the whole root system forms a spongy mass, probably in relation to the epiphytic habit of the plants.

*The Frond.*—At the base of the petiole there are two strap-shaped strands, the detailed structure of which is shown in fig. 16, B. These strands divide as they pass up the petiole in a rather irregular, but generally dichotomous, manner. The arrangement of the strands at the base of the laminal portion is shown in fig. 16, C, and this indicates that the mid-rib is formed by the union of the two inner shanks of a double dichotomy. The laminal portion itself shows up to eighteen almost vertical hexagonal areolæ. The mid-rib, which is distinguishable at the base of the lamina, dies out in the more distal portions of the frond. Spicule cells are present in the epidermis (fig. 16, D).

*Dermal Appendages.*—

The surface of the rhizome is densely clothed with clathrate scales of peculiar and characteristic form (fig. 16, A). They are relatively long and narrow, but are fixed to the rhizome by a broad base of thin-walled cells from which spring brown, unicellular, rhizoid-like structures. These latter resemble the root hairs and may possibly perform the same function.

*Sporangia.*—The sporangia are arranged in grooves situated over the longitudinally running veins and are rarely found on the transverse connections of the areolæ (Plate II, A). Paraphyses of the type shown in fig. 17, C are copiously intermingled with the sporangia. The latter are very similar in construction to those described for *Vittaria* species. They

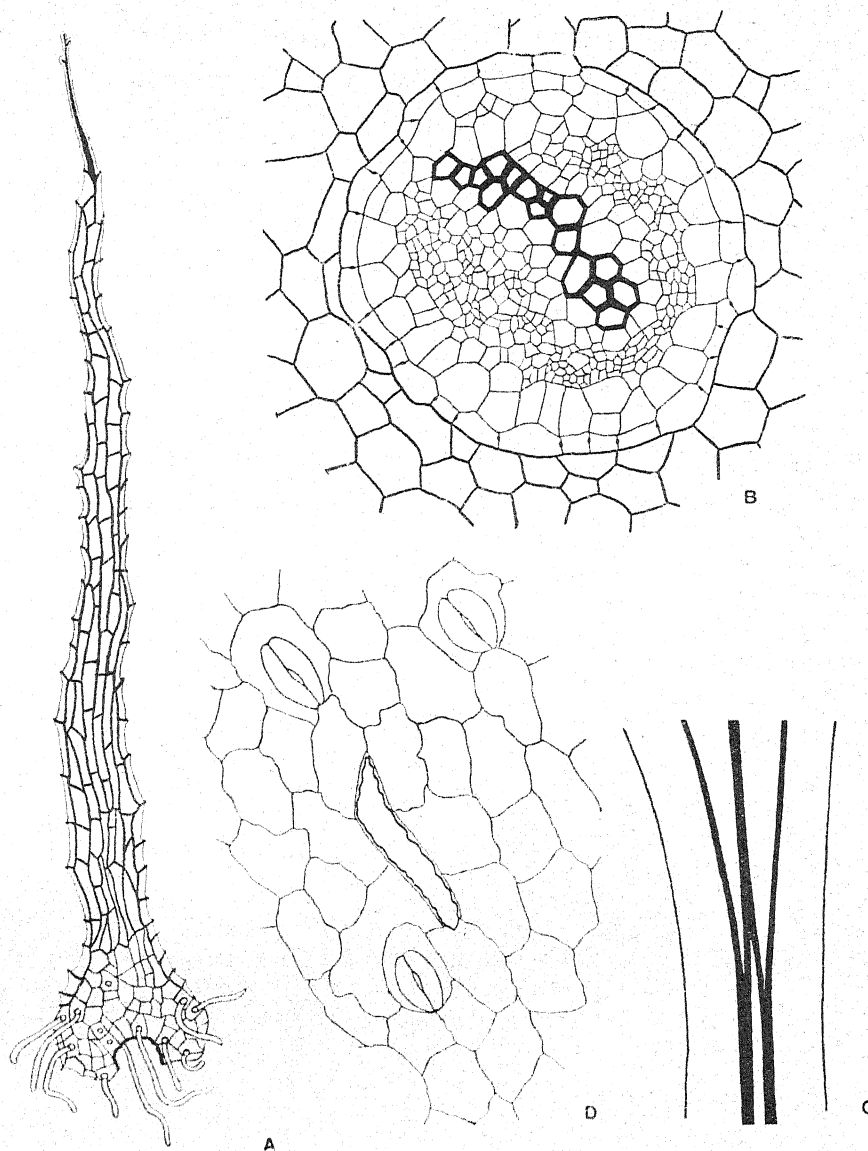


FIG. 16.—*Antrophyum reticulatum*. A, clathrate scale ( $\times 52$ ). B, one of the two strands at the base of the petiole ( $\times 265$ ). C, arrangement of the vascular strands at the base of the laminal portion. D, small spicule cell and stomata ( $\times 435$ ).

possess a four-celled stomium and an epi- and hypo-stomium each consisting of two or three cells. The stalk is similar to that described for *Vittaria* sporangia, being one-celled at its base and dilated just below the capsule (fig. 17, A). Spore counts yielded the numbers 58, 58, and 59, indicating that 64 is probably the typical number for each sporangium. The spores are tetrahedral in form (fig. 17, B).

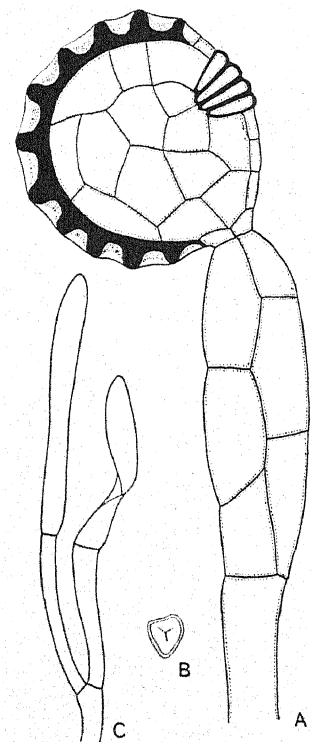


FIG. 17.—*Antrophyum reticulatum*. A, sporangium. B, spore. C, paraphysis. (All  $\times 200$ .)

*Antrophyum plantagineum* (Cavan), Kaulf.

This species has a wide distribution, it being described by HOOKER as occurring in Ceylon, Himalayas, Malay, the Philippine and Polynesian Islands. The general form of the species is shown in Plate II, B, and it will be seen that it closely resembles *A. reticulatum*. The fronds are from 6–9 inches long and from  $1\frac{1}{2}$ –2 inches broad. They are inserted in a rather irregular manner on the dorsal side of the creeping rhizome, and are closely crowded together.

*Anatomy*.—The creeping rhizome is a fleshy structure, the ground tissue being entirely parenchymatous. The anomalous stelar structure of this species has received brief mention from various writers, notably GWYNNE-VAUGHAN\* and TANSLEY,† who both regard it as being reduced; and by JEFFREY,‡ who states that the peculiar features are to be “considered as indications of specialisation away from the usual concentric tubular type of central cylinder.” The descriptions given by the above writers are very brief and omit several points of interest, so that a more complete description may now be given.

In a transverse section through an internode the stele appears as a cylindrical structure which is very small compared with the diameter of the rhizome (fig. 18, A). The xylem is in the form of a ring, one or two tracheids in thickness, and in which no definite protoxylem elements can be distinguished. Outside the xylem ring in centrifugal order are the following: a sheath of parenchyma; a more or less complete ring of phloem (composed of very small elements, very similar in appearance to the protophloem of other Ferns); a pericycle of one to three layers of large cells; and an endodermis which is in the primary condition, showing a not very clearly defined Casparian strip. The interior of the xylem ring is occupied by parenchyma, though there are a few phloem elements in a dorsal position; no internal endodermis is present (fig. 19). The method of leaf-trace departure is indicated in fig. 18, B–F. There is an endodermal pocket formed at the node, and, during the departure of the leaf-trace, no connection is established between the cortex and the pith. The xylem ring remains open for a short distance, but it is closed again before the next leaf-trace departs. The C-shaped trace consists of a crescentic band of xylem with phloem on both sides of it, the whole being surrounded by endodermis. After passing rapidly through the cortex this trace divides to give the two strands which are present at the base of the petiole.

*The Frond*.—The frond has a reticulate venation very similar to that of *A. reticulatum*. There is no definite mid-rib except in the proximal portion of the lamina. The venation of

\* GWYNNE-VAUGHAN, *loc. cit.*, p. 720.

† TANSLEY, *Lectures on the Filicinian Vascular System*.

‡ JEFFREY, *Trans. Roy. Soc. Lond.*, B, vol. cxcv, 1903.

the leaves of young plants is indicated in fig. 20, A-C. The earliest formed fronds have a single vein; a number of the next formed ones show a simple dichotomous structure, though even at this stage the two shanks of the dichotomy are united at their tips to form a single

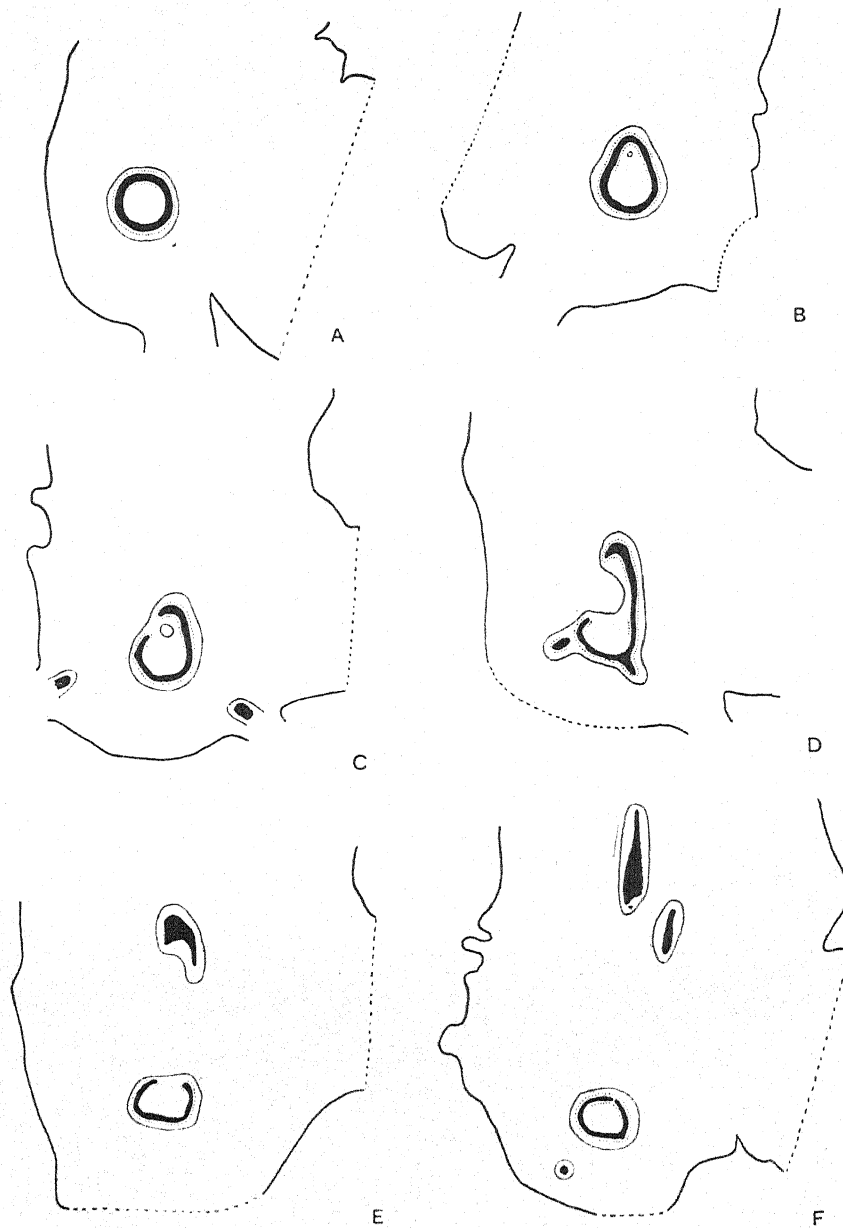


FIG. 18.—*Antrophyum plantagineum*. A-F, series of transverse sections of a mature rhizome in sequence from below upwards. ( $\times 14$ .)

areola; in later formed leaves the reticulate condition is well established, although the underlying dichotomous plan of construction is still evident. An interesting feature in the structure of the earlier formed fronds is the way in which the spicule cells are arranged round the margin (fig. 20, D). This suggests that the function, or, at any rate, one of the functions, of the spicule cells is the prevention of the tearing of the leaf-margin.

*Dermal Appendages.*—The surface of the rhizome and leaf-bases is covered with clathrate scales very similar to those figured for *A. reticulatum*.



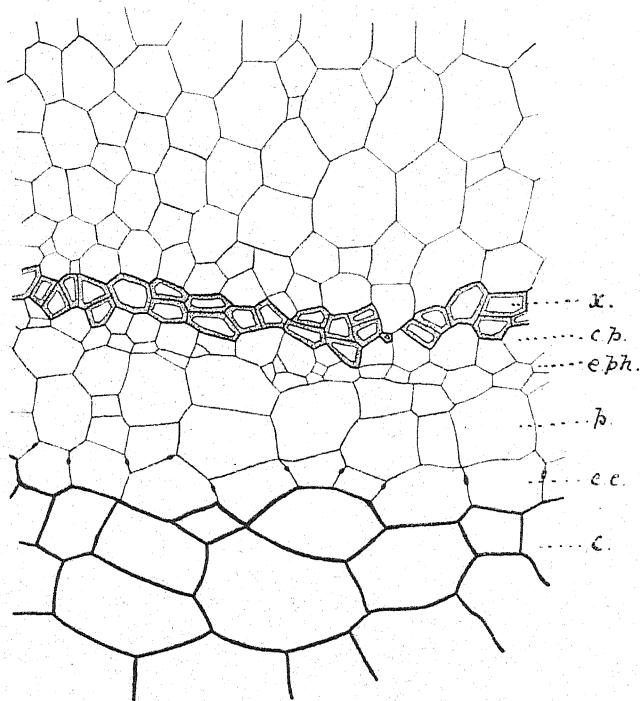


FIG. 19.—Ventral portion of the stele of *Antrophyum plantagineum*. ( $\times 265$ .)  
Lettering as in fig. 2.

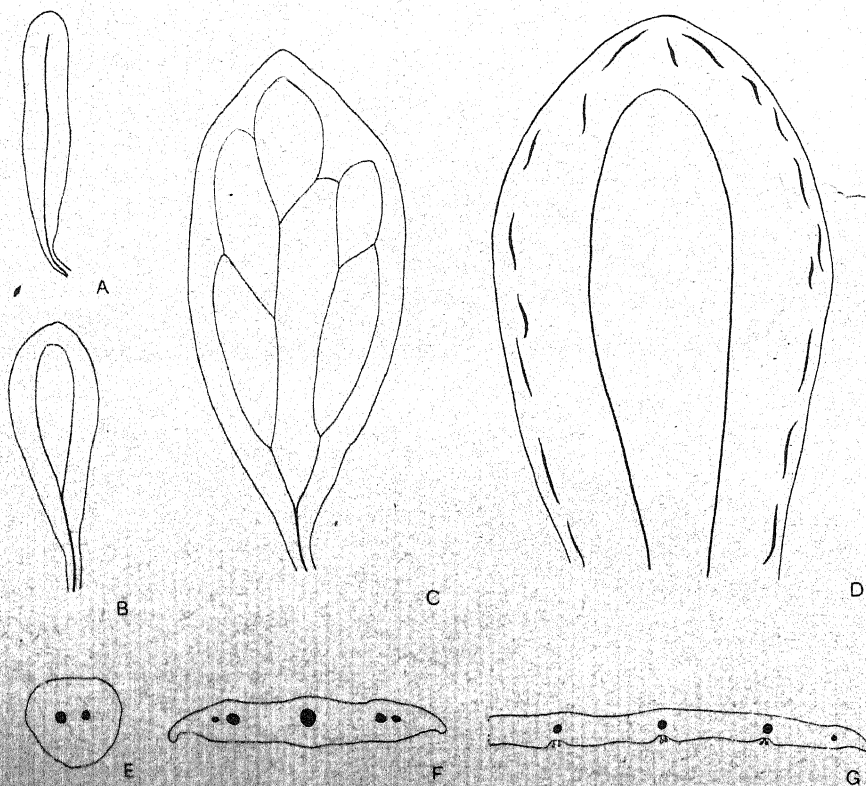


FIG. 20.—*Antrophyum plantagineum*. A–C, series of fronds of seedling plants ( $\times 4$ ). D, distal portion of frond B, showing arrangement of spicule cells ( $\times 14$ ). E, transverse section of base of petiole. F, transverse section of base of lamina. G, transverse section of middle of lamina. (E–G,  $\times 4$ .)

*Sporangia*.—The sporangial arrangement (fig. 21, A) is very similar to that described for *A. reticulatum*. The sporangia (fig. 21, B) are large and have a spore output of 56 (as indicated by spore counts which yielded the numbers 53, 54, and 56). The annulus is vertical

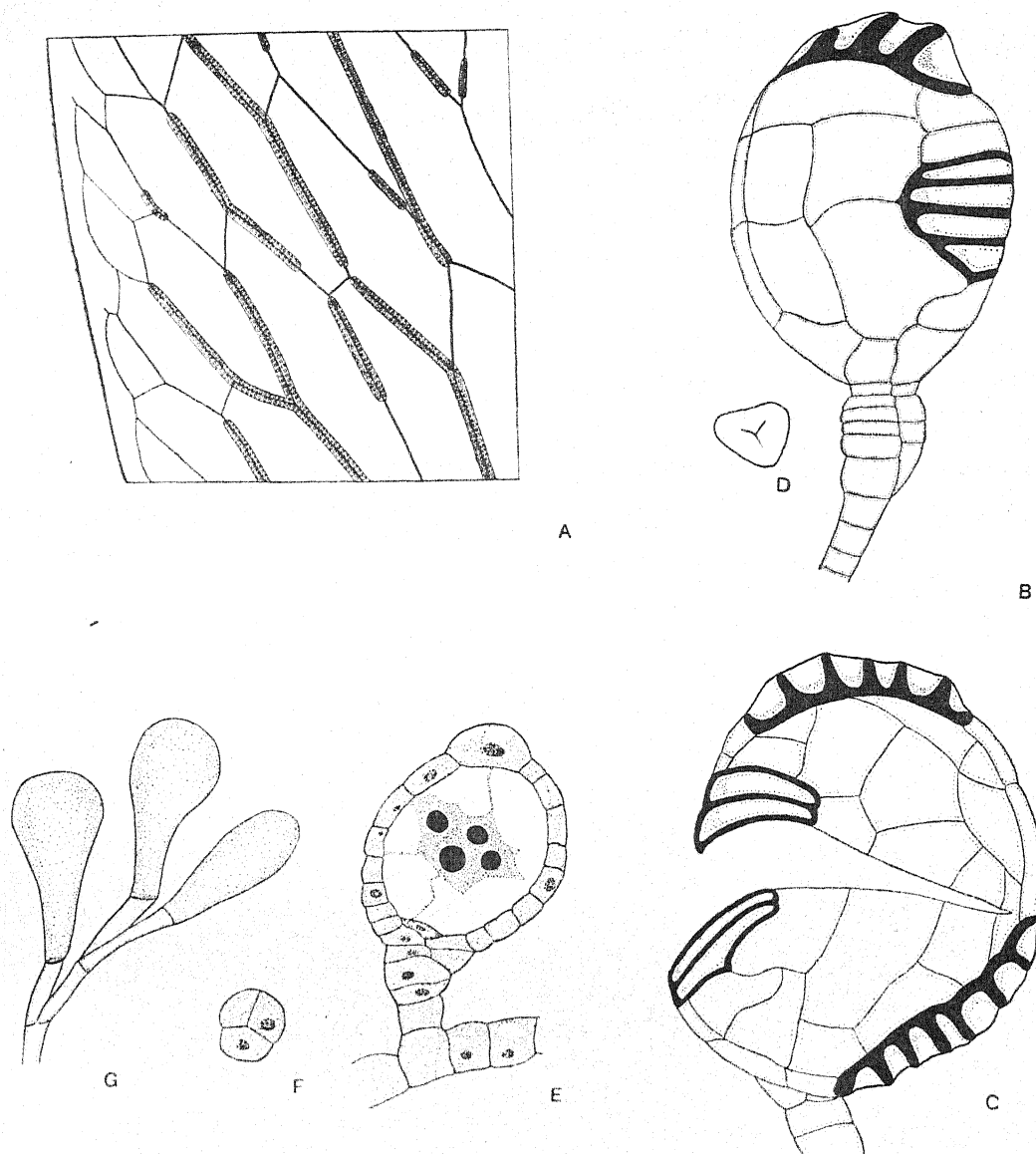


FIG. 21.—*Antrophyum plantagineum*. A, venation and sporangial distribution ( $\times 4$ ). B, sporangium. C, abnormal sporangium. D, spore. E, young sporangium. F, transverse section stalk of sporangium immediately below the capsule. G, paraphysis. (B-G,  $\times 200$ .)

and is composed of fifteen to eighteen cells; the stomium is four-celled, and there is an epi- and hypo-stomium each consisting of two cells. The stalk shows the same general features as in the sporangia of *Vittaria* species and *A. reticulatum*. The sporangial structure is very constant, but occasionally anomalous types are found such as the one delineated in fig. 21, C, where the annulus is interrupted in the middle of its length for a considerable distance. Intermingled with the sporangia are numerous branched paraphyses terminating in large club-shaped cells which are dark in colour (fig. 21, G).

*Antrophyum lineatum*, Kaulf.

*A. lineatum* (Plate II, C) is somewhat divergent from the rest of the *Antrophyum* species, and it has accordingly had a very varied systematic history. It was first described by O. SWARTZ (1788) as *Hemionitis lineata*, and the same writer later (1799) renamed it *Vittaria lanceolata*. KAULFUSS (1824) described it as *Antrophyum lineatum*, while DESVAUX (1827) placed it in the genus *Polytaenium*, and PRESL (1836) in *Loxogramme*. Most later systematists, including HOOKER, DIELS, and CHRIST, have placed it under *Antrophyum*, but BENEDICT has recently described it under the genus *Polytaenium*, Desv. The present writer, however, regards it as sufficiently similar to other *Antrophyum* species to justify its retention in that genus.

The material available for examination was collected by Professor BOWER at Holly Mount,

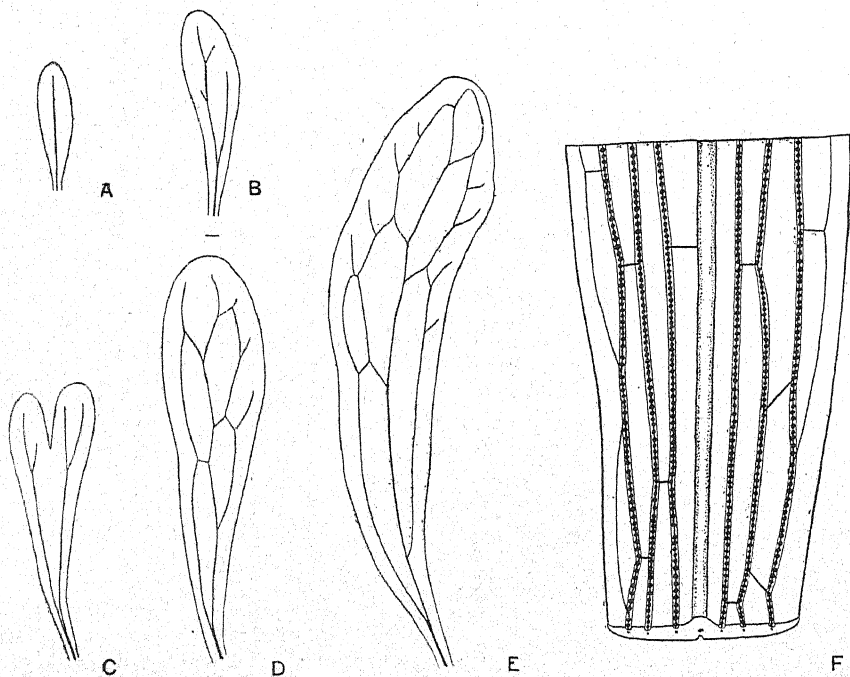


FIG. 22.—*Antrophyum lineatum*. A-E, series of fronds from seedling plants. F, venation and sporangial arrangement. (All  $\times 4$ .)

Jamaica. According to HOOKER, the range of the species is from "Cuba and Mexico to Ecuador and Brazil."

**Anatomy.**—The stele of the mature rhizome (Plate III, A) is a typical dorsiventral dictyostele with both internal and external phloem. It is similar in all essential points to that described for *A. reticulatum*, and therefore need not be described in detail. In the youngest rhizomes examined there is a very simple little protostele with at most four or five tracheids. Small single strands pass out from this into the fronds. In older rhizomes examined the dorsiventral dictyostelic condition had already been established, and intermediate stages were not observed in any of the material available for examination.

**The Frond.**—The long, narrow leaf has a distinct mid-rib and two or three rows of very long meshes on either side of it. These meshes are almost rectangular in shape, differing in that particular from other species of *Antrophyum*. A series of fronds from a young plant is shown in fig. 22, A-E. The youngest leaf has a single vein; the next formed



leaves have an open venation of a clearly dichotomous type, though in a few examples a certain degree of sympodial development is found. Older fronds show the reticulate venation established.

Spicule cells are present in the epidermis.

*Dermal Appendages.*—The dermal appendages are clathrate scales very similar in form and construction to those described for *A. reticulatum*.

The sporangia are borne in two or three distinct and almost continuous lines on either side of the mid-rib (fig. 22, F). The arrangement of the sporangia in well-defined lines is different from the condition found in other species of *Antrophyum*. The difference is due to the fact that the areolæ are almost rectangular in *A. lineatum*, whereas they are hexagonal in the species previously described. In all of them, however, the sporangia are inserted on the longitudinally running veins of the meshes. The sporangia are immersed in deep grooves with raised edges and are unmixed with paraphyses, which latter is another point of difference from the species already described. The arrangement of the sporangia in the grooves is very regular, and their orientation is such that the annulus of each is able to function efficiently in spite of their closely crowded insertion.

The sporangia themselves are very similar to those of *A. plantagineum*, showing a similarly constructed stalk, annulus, and stomium. Spore counts yielded the numbers 57 and 59, indicating that the typical spore output for each sporangium is probably 64. The ontogenetic development of the sporangia follows very closely that of other advanced Leptosporangiate types.

*Antrophyum lanceolatum*, Kaulf.

This species differs from the species previously described in the fact that the sporangia are borne superficially on the surface of the frond. The fronds, which are a foot or more in length and about half an inch broad, have a distinct mid-rib, and on this account the species is placed in the genus *Polytaenium* by BENEDICT. HOOKER describes its distribution as being from the West Indies and Mexico to New Granada. The material used in this investigation was collected by Professor BOWER in Jamaica.

*Anatomy.*—The mature rhizome possesses a dorsiventral dictyostele which is of small size in proportion to the diameter of the rhizome. In detailed construction the stele is very similar to that of *A. reticulatum* except that the internal phloem forms a complete band, not being absent on the ventral side as in the latter species. The vascular supply of the youngest rhizomes available for examination is solenostelic, each leaf-gap being closed, though only for a short distance, before the next gap opens out.

*The Frond.*—The lanceolate fronds have a very distinct mid-rib and three or four rows of hexagonal meshes on either side of it. The marginal meshes are often incomplete, showing free vein endings. Spicule cells are present only in the upper epidermis of the specimens examined, and they are mainly disposed around the margin of the frond.

*Dermal Appendages.*—The clathrate scales which cover the surface of the rhizome are of the usual *Antrophyum* type, but they are mixed with simple hairs which are not present in any of the other species examined.

*Sporangia.*—The sporangia, which are borne superficially on the longitudinally running veins, are of the same type as described for other species. Paraphyses are absent. Spore counts yielded the numbers 43 and 45, indicating that the typical number of spores produced in each sporangium is 48.

*Antrophyum brasilianum*, C. Chr.(=*A. subsessile*, Kunze.)

*A. brasilianum* may be taken as an example of a broad-leaved form with its sporangia borne superficially (fig. 23). The fronds are from 6–12 inches long and from 1–1½ inches broad.

They possess a distinct mid-rib, and on that account the species is included in the genus *Polytaenium* by BENEDICT. Its distribution is described as being from Cuba and Guatemala to Peru.

The general structural features are very similar to those of other *Antrophyum* species. A point of interest is that the mature rhizome sometimes possesses a more advanced type of dictyostele than the dorsiventral dictyostele owing to the overlapping of more than two leaf-gaps at any one level.

Spore counts yielded the numbers 43, 45, 46, and 49, indicating that 48 is probably the typical number of spores produced in each sporangium.

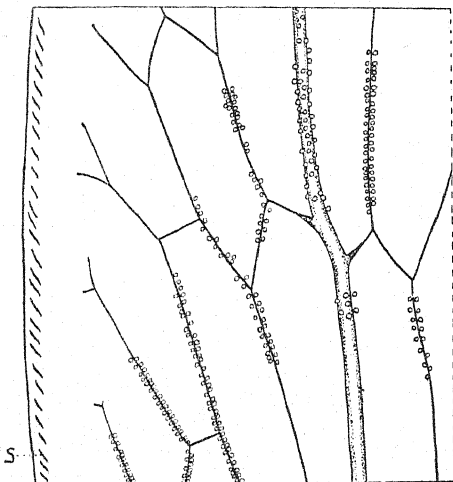


FIG. 23.—*Antrophyum brasilianum*, venation, sporangial distribution and peripheral spicule cells. ( $\times 4$ .)

frequently by root buds. The leaves may, according to HOOKER, reach a length of 1½–2 inches, but the specimens available for examination were much smaller. The leaves are characterised by the fact that they possess an open dichotomous venation, the outline of the frond also being branched in a dichotomous manner. These leaf characters are distinctly anomalous in the Vittarieæ. SPRENGEL (1828) and HOOKER (*Syn. Fil.*) included this form in §§§§ *Eugymnogramme* of the genus *Gymnogramme*, but J. SMITH had already in 1842 instituted the new genus *Hecistopteris* for its reception since, as he states in the *Historia Filicum* (1877), “it did not appear to me to form any natural alliance with any of the groups of species of that genus (*i.e.* *Gymnogramme*).” The same writer points out that certain structural features “indicate its relationship with *Monogramma* and *Pleurogramma*.” It remained for GOEBEL (*loc. cit.*, 1896) to demonstrate clearly the soundness of separating *Hecistopteris* from *Gymnogramme*, and also the affinity of this form with the other genera of the Vittarieæ on the basis of the anomalous structure of the gametophyte, the presence of spicule cells and the absence of sclerenchyma from the shoot axis.

The following account is based on specimens from the Herbarium of the Royal Botanic Garden of Edinburgh, kindly sent to me by Professor WRIGHT SMITH. The label accompany-

## HECISTOPTERIS, J. Smith.

*Hecistopteris pumila* is an extremely small form having a slender creeping rhizome and reproducing frequently by root buds. The leaves may, according to HOOKER, reach a length of 1½–2 inches, but the specimens available for examination were much smaller. The leaves are characterised by the fact that they possess an open dichotomous venation, the outline of the frond also being branched in a dichotomous manner. These leaf characters are distinctly

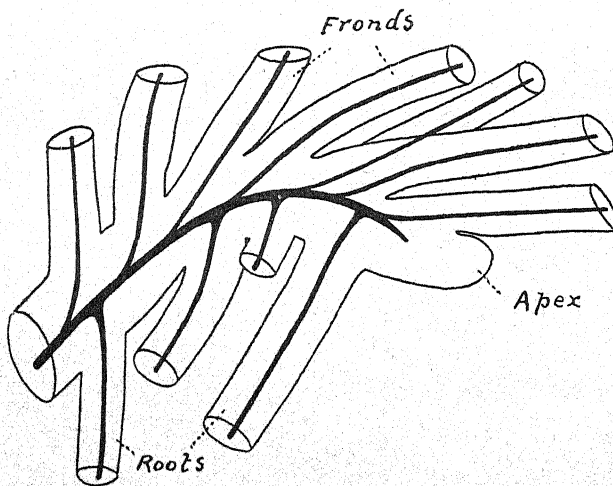


FIG. 24.—*Hecistopteris pumila*. Portion of rhizome cleared in Eau de Javelle and stained with basic fuchsin, showing general course of vascular strands.

ing the specimens is as follows: "Plants of Trinidad. No. 132. *Gymnogramme pumila*, Anton Sprengel. Legit A. Fendler, 1877-80."

*Anatomy*.—The material did not soak out sufficiently well to allow of any detailed anatomical study. It was possible, however, to verify GOEBEL's statement that the stelar structure of the rhizome is very similar to that of *Monogramma* species. Indeed, in the small specimens available for examination, the stele is even simpler than that of the *Monogramma* species examined. It consists of a small protostele, oval in outline, and possessing a short bar of xylem. The leaf-traces depart from this as very small and simple strands. The general course of the vascular strands in the rhizome is shown in fig. 24, which is a slightly diagrammatised drawing of a length of rhizome cleared in Eau de Javelle and stained with ammoniacal fuchsin.

*The Frond*.—The first-formed fronds of young plants are single-veined, but even at this stage the outline of the frond shows a distal dichotomy (fig. 25, A). Later formed fronds show a single dichotomy (fig. 25, B), while the fronds of older plants exhibit a repeated dichotomy of the veins, the latter remaining free and ending in little bundles of tracheids (fig. 25, D-G). The outline of the frond itself follows the plan of the venation, although the distal dichotomies of the frond are often in excess of the number of vein-endings.

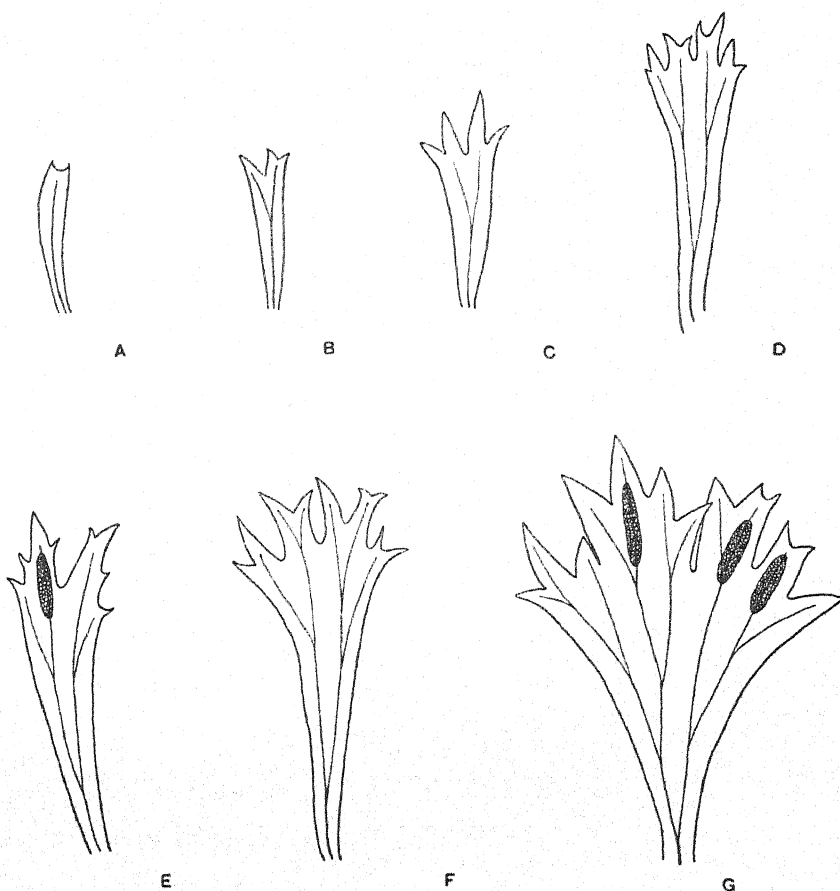


FIG. 25.—*Hecistopteris pumila*. A-G, series of fronds from plants of different ages, E and G showing sori.

Numerous long spiculate cells are present in the epidermis and, apart from giving mechanical rigidity to the frond as a whole, their arrangement suggests that they also prevent tearing of the leaf-margin.

*Dermal Appendages*.—The surface of the rhizomes and leaf-bases is clothed with small clathrate scales (fig. 26, E). They have very thick walls and are inserted on the rhizome by a broadened base.

*Sporangia*.—The fronds reach a fertile condition at a very early stage, as is shown by fig. 25, E, which is a drawing of the frond of a young plant with only a double dichotomy, but which already possesses a sorus along one of its veins.

The sporangia themselves are very similar to those of other genera of the Vittarieæ (fig. 26, A and B). The annulus is vertical and consists of sixteen to twenty cells. The stomium is usually four-celled, but in some of the specimens examined it was five-celled. The stalk is single-celled below, but is dilated just below the capsule. It was impossible to determine



the exact constitution of the stalk owing to the poor preservation of the material. The spores (fig. 26, C) are tetrahedral in form, but no spore counts were possible. The sporangia are mixed with branched paraphyses (fig. 26, D) of the usual Vittarieaceous type, the branches ending in swollen, club-shaped cells.

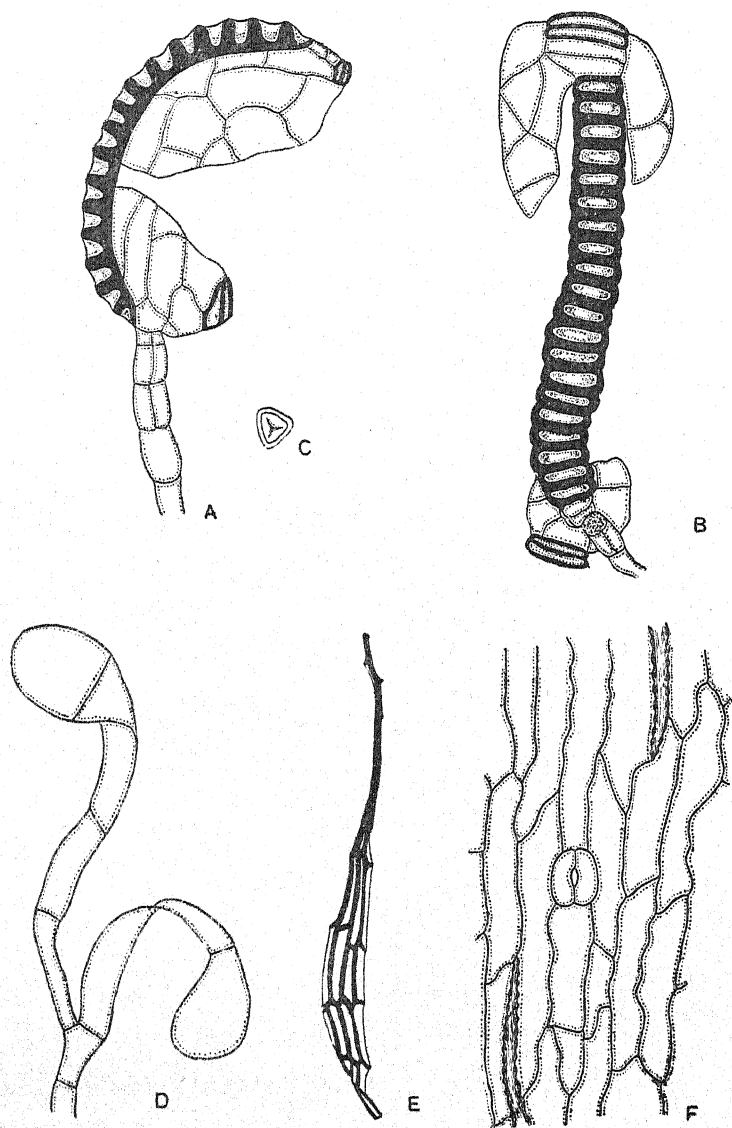


FIG. 26.—*Hecistopteris pumila*. A and B, sporangia. C, spore. D, paraphysis. (A–D,  $\times 200$ .) E, clathrate scale ( $\times 55$ ). F, portion of epidermis with stoma and portions of spicule cells ( $\times 200$ ).

#### ANETIUM, Splitgb.

*Anetium* is a curious and anomalous monotypic genus which has undergone various vicissitudes of classification. Originally named *Acrostichum citrifolium* by LINNÆUS, *Anetium citrifolium* has since been described under various generic names. PRESL placed it under §2 *Antrophyum* of the genus *Hemionitis* as *H. spatulata*. FÉE placed it in the genus *Antrophyum*, while HOOKER placed it again under *Hemionitis* as §§ *Anetium*, remarking that it is “an anomalous species, with the habit of *Antrophyum*.” JOHN SMITH and most later systematists have described it under *Anetium*, Splitgb. GOEBEL and, more recently, Frau SCHUMANN have emphasised its relationship with the other genera of the Vittarieæ, mainly on the basis of its general form and the fact that spicule cells are present in the frond. It is an epiphytic form of the West Indies, usually growing in very moist situations. It has a comparatively

slender creeping rhizome, on which simple pendent leaves are inserted in two rows at rather distant intervals. Branching of the rhizome appears to be infrequent, but does occur occasionally. The material upon which the following description is based was collected by Professor BOWER in Jamaica.

**Anatomy.**—*Anetium citrifolium* is more advanced in its anatomical construction than any other genus of the Vittarieæ. It is very different from the other genera both in its gross stelar morphology and in anatomical detail. The mature rhizome is fleshy and about a quarter of an inch in diameter; the amount of vascular tissue present is relatively very small.

In any internode two or sometimes three meristemes are present (fig. 27, B–D). Of these, one is considerably larger in size, and this is situated in a ventral position, while the other one or two meristemes are smaller and are dorsally situated. The structure of the large ventral

meristele, from which the root-traces depart, is as follows (fig. 28, C). The xylem is in the form of a shallow U-shaped curve one or two tracheids in thickness and frequently not continuous. The walls of the tracheids are thin and only slightly lignified. Phloem is present on both sides of the xylem curve and consists of small elements whose walls stain deeply with hæmatoxylin. The meristele is surrounded by a one- to several-layered pericycle and an endodermis which is in the primary condition, showing an ill-defined Casparian strip. The structure of the small dorsal meristele is very similar to this, except that the xylem is in the form of a straight bar of tracheids.

The gross morphology of the stele is anomalous and difficult to relate to any of the types of stele usually present in the Ferns. It varies in detail in different rhizomes, but in the specimens examined it is in the form of a dictyostele complicated by perforation. The general

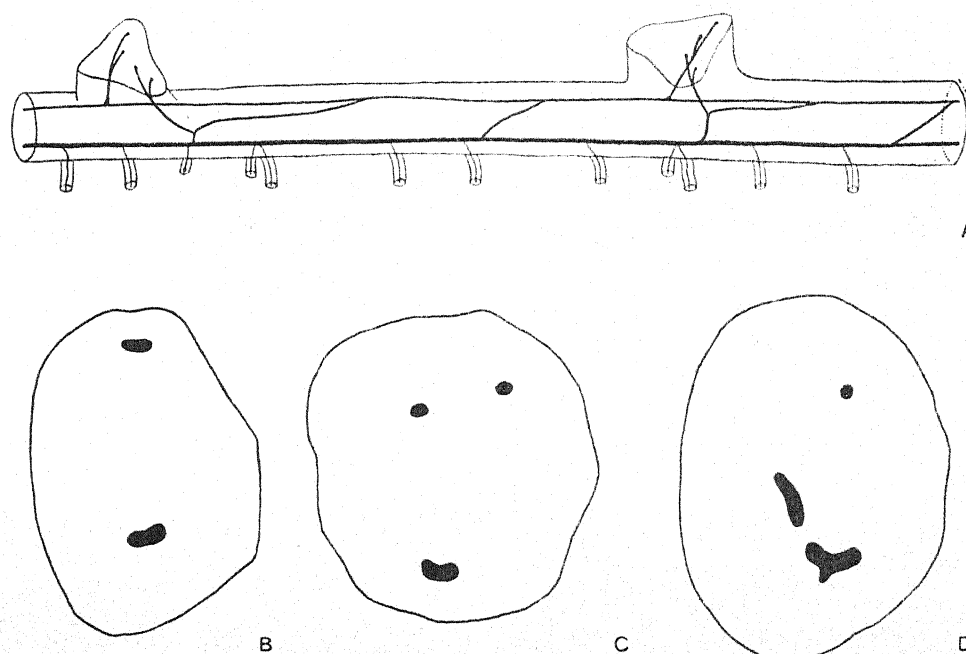


FIG. 27.—*Anetium citrifolium*. A, a length of rhizome showing the general course of the vascular strands. B-D, transverse sections of the rhizome. ( $\times 14$ .)

appearance of the stele in a length of rhizome is shown in fig. 27, A, drawn from a model built up from successive hand sections, and the structure of the stele at a node a little way back from the apex is shown in Plate III, B. The leaf-trace departs as two strands, one from each side of the leaf-gap, and these divide while still in the cortex into four strands which divide again in the base of the petiole. A section across the base of the petiole shows a shallow horse-shoe curve of strands with the open end of the horse-shoe to the adaxial surface.

The stele of seedling plants is in the form of a simple protostele (fig. 28, A). The xylem consists of a very small group of tracheids around which there are in centrifugal order: a sheath of large-celled parenchyma; a broken ring of phloem elements; a one- to several-layered pericycle and an endodermis. The leaf-traces are given off from this protostele as single, small, and simple strands without disturbing the xylem. The protostelic condition persists through a considerable length of rhizome. The xylem extends somewhat and forms a shallow U-shaped curve, resembling in miniature that of the ventral meristele of the mature rhizome (fig. 28, B). Even at this stage the leaf-traces depart alternately from the right- and left-hand side of the stele as single strands whose departure does not disturb the xylem of the axial stele. The

material available did not allow of the observation of the transition from the protostelic condition to the more complex structure of the mature rhizome. In rhizomes of slightly

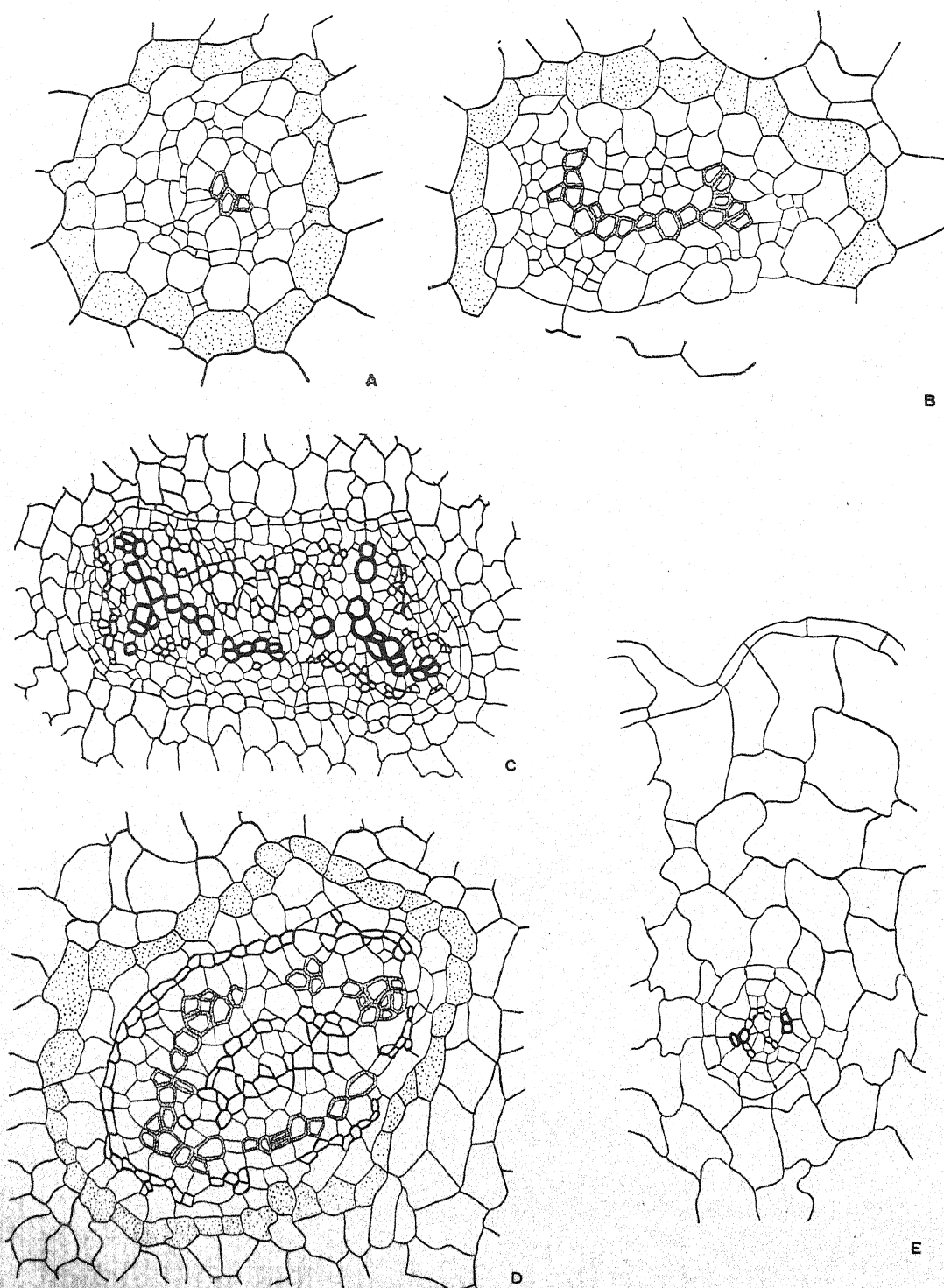


FIG. 28.—*Anetium citrifolium*. A and B, stele of young plant; description in text ( $\times 430$ ). C, ventral meristele of mature rhizome ( $\times 155$ ). D, stele at the base of a branch ( $\times 265$ ). E, sector of root ( $\times 265$ ).

larger diameter than those just described, however, the dictyostelic condition is already established, and it seems highly probable that the protostele passes directly to the dictyostelic



condition. A sufficient number of young rhizomes were examined to render it extremely unlikely that any intermediate conditions occur.

Branching has been observed in a number of rhizomes of different ages, though in all the examples which were sectioned the stele had already attained the dictyostelic condition. These branchings are not, as far as could be determined, related in any way to the insertion of the leaves, and must be regarded as essentially dichotomous though showing an unequal development of the two shanks. Fig. 29, A-E represents a series of sections taken in the region of branching and indicates the unequal nature of the division of the vascular supply. As the level of branching is approached changes take place in the conformation of the large

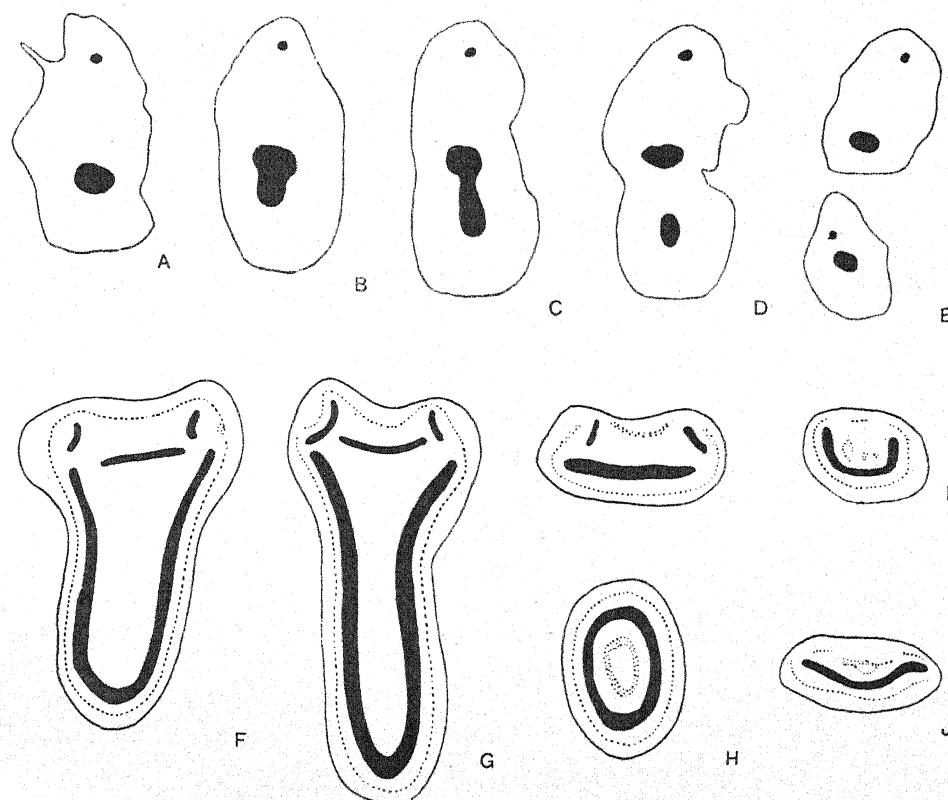


FIG. 29.—*Anetium citrifolium*. A-E, series of transverse sections in the region of branching of a young rhizome ( $\times 14$ ). F-H, stele at levels of B, C, and D. I and J, branch stele (F-J,  $\times 65$ ).

ventral meristele with the result that it assumes the curious conformations shown in fig. 29, F, G, and finally the smaller branch-trace is abstricted off (fig. 29, H). One arm of the branching continues with its vascular supply still dictyostelic and closely resembling that of an unbranched rhizome. The stele of the other branch (fig. 28, D) is unlike anything observed in the structure of unbranched rhizomes, either in the mature condition or in the ontogenetic stages. The xylem is in the form of a broken ring of relatively large tracheids. The centre of the stele is occupied by parenchyma mixed with tissue, the walls of which stain deeply with hæmatoxylin and which is probably internal phloem. No internal endodermis is present. Outside the xylem is a practically complete band of phloem, and the whole stele is surrounded by a somewhat irregular endodermis in the primary condition. In the material available for examination it was unfortunately not possible to observe the departure of any leaf-traces from this branch stele. Further along the branch changes take place in the conformation of the vascular strand. The xylem ring becomes broken on the dorsal side and appears first

as a U-shaped curve, and later as an almost flat plate (fig. 29, I and J). It was impossible to determine whether the branch stele ever becomes dictyostelic.

*The Frond.*—The fronds measure up to 9 inches long and 2 inches broad and are shortly petiolate. At the base of the petiole a shallow horse-shoe curve of strands is present, the two central ones moving together at a higher level to form the mid-rib which remains distinct except in the distal portions of the frond (fig. 30, D and E). Eight or nine hexagonal meshes are present on either side of the mid-rib, the marginal ones being incomplete and showing free vein-endings. Spicule cells (fig. 31, A and D) are scattered throughout the upper epidermis and a number of very large ones are arranged round the periphery, presumably for the purpose of preventing tearing of the leaf-margin.

The venation of the fronds of young plants is indicated in fig. 30, A-C. No stage was observed in which only a single vein is present, which is a point of difference from the fronds

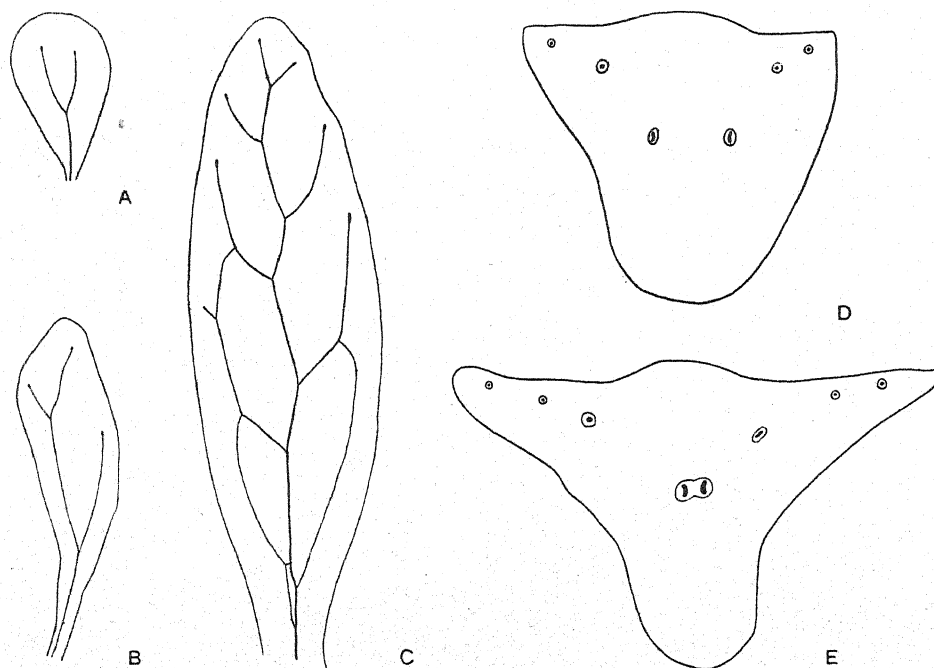


FIG. 30.—*Anetium citrifolium*. A-C, series of fronds of young plants ( $\times 4$ ). D, transverse section at the base of the petiole ( $\times 14$ ). E, transverse section at the base of the lamina ( $\times 14$ ).

of seedling plants of *Vittaria*, *Antrophyum*, and *Hecistopteris*. The first frond shows a simple dichotomy, while subsequent fronds show a sympodial development, and finally the establishment of the reticulate venation characteristic of the fronds of mature plants. The surface of the fronds of young plants bears what are presumably glandular hairs. These are small club-shaped structures consisting of about three cells with dense granular contents (fig. 31, D). Similar hairs have been described as occurring on the fronds of *Vittaria lineata*.

*Root Structure.*—The roots arise in an irregular manner all round the ventral side of the rhizome. They resemble those of other *Vittarieæ* in that they are densely clothed with brown root hairs. The structure of the root stele is exceedingly simple (fig. 28, E). There are two groups of lignified elements each consisting of one or two tracheids, and two small groups of phloem alternate with these. The stele is surrounded by a large-celled pericycle and an endodermis. The cortex is entirely parenchymatous.

*Superficial Appendages.*—The surface of the rhizome and leaf-bases is clothed with very broad clathrate scales, similar to those of *Antrophyum* species except that their walls are much

less strongly thickened. As in the scales of *Antrophyum* species, the cells at the base remain thin-walled and give rise to rhizoid-like structures.

*Sporangia*.—The arrangement of the sporangia is peculiar and anomalous, and has attracted attention for a considerable time. The sporangia are inserted in small groups superficially, both over the veins and on the intervening parenchyma of the areolæ (fig. 31, A). Each group of sporangia is situated on an area of very small cells, which arise, according to Frau SCHUMANN,\* in the following manner: A group of three or four epidermal cells divide by walls parallel to the surface. In the outer cells cut off in this way anticlinal walls are formed, so that a group of very small cells is produced. It is from these cells, which possess densely granular contents, that the sporangia arise (fig. 31, C).

The individual sporangia (fig. 31, B) are very small compared with those of *Antrophyum*. They are short-stalked, the stalk being three-celled below the capsule but tapering down to a single cell at its base. The annulus is vertical and consists of twelve to fourteen cells. As in other Vittarieæ, the stomium consists of four cells and the epistomium of two cells. The spores are tetrahedral in form. Spore counts yielded the numbers 29, 32, 30, and 46, indicating that there are typically 32 or 48 spores produced in each sporangium.

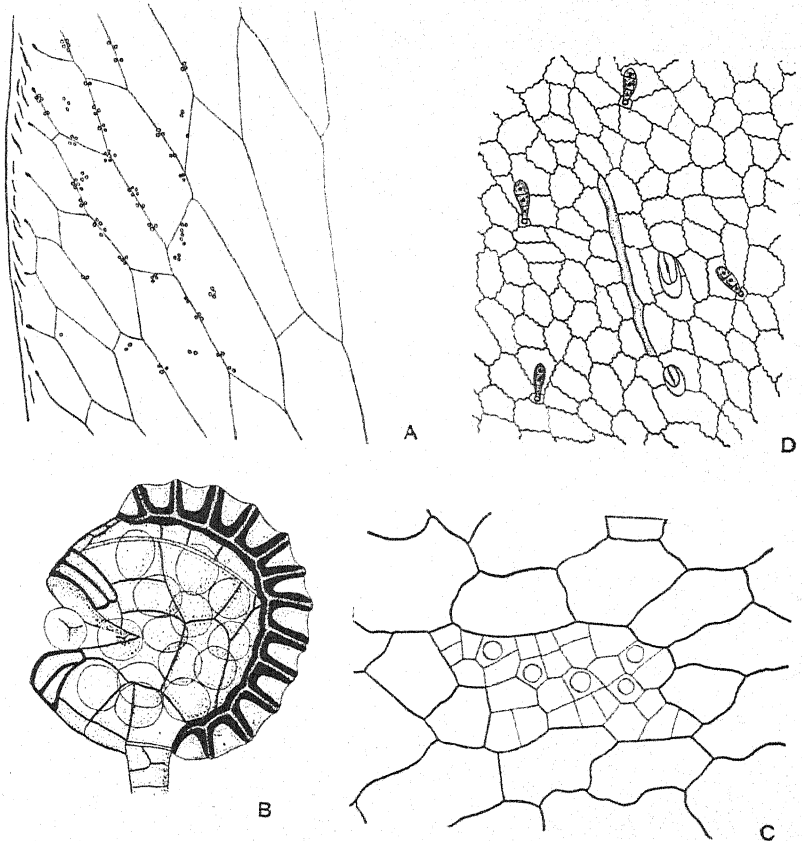


FIG. 31.—*Anelium citrifolium*. A, portion of frond showing venation and sporangial distribution and peripheral spicule cells ( $\times 4$ ). B, sporangium ( $\times 200$ ). C, group of small epidermal cells from which the sporangia arise ( $\times 200$ ). D, portion of lower epidermis showing stomata, a spicule cell, and glandular hairs.

#### THE GAMETOPHYTE.

The structure of the gametophyte of Ferns is so simple and shows so little differentiation in its tissues that it does not usually provide many characters of importance for systematic comparison. This is particularly the case in the more specialised groups of Ferns where the prothallus is almost always of the heart-shaped type, though liable to modification under the action of various environmental conditions. Professor BOWER† has already pointed out that "the form and physiology of the prothallus may provide material for comparison, though this is not very reliable since it varies readily and often directly with the external conditions."

The prothalli of the Vittarieæ, in the three genera where they are definitely known, are

\* SCHUMANN, "Die Acrosticheen und ihre Stellung im System der Farne," *Flora*, N.F. 8.

† BOWER, F. O., *Filicales*, vol. i, p. 62.



epiphytic, and it is not surprising, in view of the plasticity already mentioned, that they all show characters divergent from the common cordate type. The prothalli of *Vittaria*, *Monogramma*, and *Hecistopteris* have been accurately investigated, chiefly by GOEBEL\* and, in the case of *V. lineata*, by BRITTON and TAYLOR.† In all of them the prothallus is a very irregularly lobed structure and vegetative reproduction by proliferation, and the production of gemmæ is a characteristic feature. The archegonia and antheridia do not diverge from the usual Leptosporangiate type.

Nothing definite is known concerning the prothalli of *Antrophyum* and *Anetium*.

#### STELAR PROBLEMS.

The steles of the Vittariæ have attracted attention for a considerable time on account of the fact that they frequently exhibit divergences from the more common types of Fern steles. POIRAULT, JEFFREY, GWYNNE-VAUGHAN, and TANSLEY have all given brief descriptions of the steles of various species of the Vittariæ, and in all cases they regard the divergences from typical solenostelic or dictyostelic structure as being due to reduction. The occurrence of such anomalous steles has a direct bearing on certain problems of stelar morphology, but before proceeding to discuss the problems involved it is necessary to define exactly what is meant by the term "reduction." The term, as usually used, implies the loss of tissues originally present, due, presumably, to a change in the physiology of the plant consequent upon a change of habitat. In the questions under consideration it is necessary to distinguish between:

(a) Reduction which results in the diminution of the amount of xylem and phloem present in the stele, without, however, the general type of the stele being altered.

(b) Reduction which results in the disappearance of either the internal or external endodermis, thereby leading to an alteration of the type of stele.

Reduction appears to have affected the xylem of all the Vittariæ examined to the extent of reducing it to a ring of tracheids only one or two layers in thickness. The amount of phloem present is also small and consists entirely, so far as I have been able to distinguish, of small protophloem-like elements, which, however, have the typical structure of Filicinean sieve tubes. Here again it is probable that reduction has led to a diminution in the amount of tissue present. With reference to the absence of internal phloem on the ventral side of the stele in such forms as *Antrophyum reticulatum* and a number of *Vittaria* species, it is difficult to decide whether this is the result of reduction or whether it is due to the fact that the pocketing in of the phloem at the nodes has never extended to the ventral side of the stele. It is, in any case, a small point of no particular importance. The reduction in the amount of xylem and phloem may possibly be correlated with the epiphytic habit, but, so far as I am aware, the physiology of such forms with large fleshy leaves and relatively small axes has never been examined.

The main interest in this question of reduction centres round the curious forms of stele found in *Antrophyum plantagineum* and *Vittaria elongata*. The absence of internal endodermis in these steles is the critical point, and the question raised is as to whether or not reduction is responsible for this absence with the consequent change in the type of stele. POIRAULT states in his description of the stele of *Vittaria elongata*: "J'ai vu de même l'endoderme très distinct à la face externe de la stèle, tout à fait indistinct à la face interne,"

\* GOEBEL, *Ann. Jard. Bot.*, vii, pp. 78-87.

† BRITTON and TAYLOR, *Mems. Torrey Bot. Club*, vol. viii.

and he states elsewhere that the internal endodermis has lost its distinctive characters. It is not altogether clear whether POIRAULT regarded the internal endodermis as having been present originally and lost by reduction or not, and apart from mentioning his statements they will not be brought further into the discussion. JEFFREY, however, definitely regarded the peculiar structure of the steles as "indications of specialisation away from the usual tubular type of central cylinder," and it is clear that an actual loss of the internal endodermis by reduction was contemplated. GWYNNE-VAUGHAN, as has been previously mentioned, has given brief descriptions of a number of *Vittaria* and *Antrophyum* species, and he clearly regarded their steles as showing reduction, though he makes no definite statement as to its extent. This writer points out in his discussion of the primitiveness or otherwise of the *Lindsaya* type of stele that there are certain differences between the latter and the anomalous steles of the Vittarieæ. These differences he regarded as important in the arguments advanced in support of the thesis that the *Lindsaya* type is primitive and that it has not arisen as a result of the reduction of a more complex type. It appears from the general trend of this argument that GWYNNE-VAUGHAN actually regarded the anomalous steles of the Vittarieæ as having resulted from the reduction of typical solenosteles and dictyosteles, the reduction involving the loss of the internal endodermis. TANSLEY has also stated that the anomalous steles under consideration are reduced structures (*The Filicinean Vascular System*, p. 65).

There appears, then, to be a consensus of opinion that the steles of *Antrophyum plantagineum* and *Vittaria elongata* are modifications of more complex types of stele by reduction. Opinions have varied, however, and, indeed, have never been really definitely stated, as to what weight can be given to this evidence in a consideration of the question of medullation and the related question as to the primitiveness or otherwise of the medullated protostele. The general question of the origin of the pith need not be entered into in this memoir; it has already received adequate attention elsewhere.\* The related question as to the primitiveness of the medullated protostele has also been satisfactorily settled on the basis of evidence derived from a study of the ontogeny of a number of different Ferns and from a study of the fossil record of the Osmundaceæ. It is true, nevertheless, that while the belief is held that the stelar structure of such forms as *Antrophyum plantagineum* and *Vittaria elongata* has resulted from the operation of reduction processes leading to the loss of the internal endodermis, then these structures must be accepted as evidence as to the possibility of the medullated protostele being, in some cases at any rate, the product of reduction. The view that the medullated stele is the product of reduction is not now generally accepted, but it is still upheld by JEFFREY. The latter writer states that "The simplest view, and that most in harmony with all the facts, seems to be that the medullated monostelic central cylinder, so strikingly characteristic of the more modern vascular plants, has been derived from an ancestral siphonostelic condition with internal phloem by reduction."† Elsewhere the same writer speaks of the origin of the medullated protostele from the siphonostelic condition "through the loss of internal phloem and endodermis."‡ It seems worth while therefore to discuss briefly the question as to whether, in the steles of the Vittarieæ, reduction has led to the loss of internal endodermis, with the consequence that a medullated type of stele has arisen from a solenostelic or dictyostelic type.

If the endodermis has merely lost its distinctive characters, such as the Casparian strip, by reduction, then it might be expected that its position could still be detected by reason

\* BOWER, F. O., *Filicales*, vol. i. p. 124 *et seq.*

† JEFFREY, *loc. cit.*, p. 143.

‡ JEFFREY, *The Anatomy of the Woody Plant*, p. 291.

of the shape and definite arrangement of the line of cells, and, further, by the presence immediately inside it of a layer of pericycle, which latter layer is strongly developed in other Vittarieæ. In neither *Antrophyum plantagineum* nor *Vittaria elongata* can any such indication of a degenerate endodermis be found. On the basis of this negative evidence one may conclude, though without certainty, that the internal endodermis has never been present in these steles, and that consequently the similarity to a medullated protostele is not due to a process of reduction. It must be admitted, however, that this evidence is by no means conclusive, for the endodermis in other species of the Vittarieæ is very irregular, and it is also possible that the internal pericycle has lost its distinctive characters.

More satisfactory evidence as to the real nature of the anomalous steles under consideration is provided by the facts relating to the ontogeny of *Antrophyum reticulatum* which have been described above. It is necessary to consider here the steles of *Antrophyum plantagineum* and *Vittaria elongata* separately. If we take *A. plantagineum* first and consider it in the light of the ontogeny of *A. reticulatum* a very important fact emerges. The solenoxyllic condition of the stele of *A. plantagineum* is identical with the structure of the stele in some of the lower internodes of the young plant of *A. reticulatum*. This at once brings to mind similar examples, as, for instance, in the Schizaeaceæ where the adult structure of the stele of *Schizaea rupestris* is very similar to an ontogenetic stage in the development of the dictyostelic condition of *Anemia phyllitidis*. In this example it is now generally accepted that the stele of *Schizaea rupestris* is not a reduced structure but a primitive one. In *A. plantagineum* also it appears probable that the stele is either truly primitive or else it is simple as a result of "arrested development." It is impossible to decide with certainty which of these two alternatives is correct. Evidence from other characters points to the conclusion that *A. plantagineum* cannot be regarded as a primitive type, and it therefore seems probable that the stele of this form is simple by an arrest of the normal ontogeny which leads in other species to the establishment of the dorsiventral dictyostele.

The type of stele present in *Vittaria elongata* offers rather more difficulty. The structure of the stele of this species has not been observed in the ontogeny of related forms, so that it cannot be explained as a simple arrested development. The dorsiventral dictyoxyllic condition is, however, probably to be regarded as a further modification of the solenoxyllic condition of *A. plantagineum*, although it is off the usual track of ontogenetic development as described for other Ferns. The change from the solenoxyllic to the dictyoxyllic condition is probably consequent upon either an increase in the size of the leaf-gaps or else a shortening of the internodes. The size of the respective steles may also be one of the factors concerned; this point will be mentioned again below.

The conclusion of the present writer is therefore that the somewhat anomalous steles of the two species just considered are not to be explained as having been derived from more complex steles by a process of reduction. The solenoxyllic stele of *A. plantagineum* is really an arrested development; that of *V. elongata* is a further development of the *A. plantagineum* type along an unusual line, not progressing to typical solenostely or dictyostely but to a dictyoxyllic condition. This conclusion, if it be correct, destroys evidence which has hitherto pointed to the possibility of explaining the medullated protostele as a reduced structure, derived from the solenostelic type of stele by the loss of internal phloem and endodermis.

There remain to be considered the steles of *Monogramma* and *Hecistopteris*. A comparison of these with the early stages of the development of the stele of *A. reticulatum* suggests at once that they are not reduced structures, but that they may be reasonably regarded as arrested developments, the arrest having come into operation at an early stage.



## THE OPERATION OF THE SIZE FACTOR.

The Vittarieæ present a series of forms which show in their mature rhizomes stelar structures ranging from protosteles in *Monogramma* and *Hecistopteris* to a perforated dorsiventral dictyostele in *Anetium*. It has been pointed out in the discussion of the stelar problems that some of the "simpler" types of stele may best be regarded as arrested developments of the normal ontogeny which leads in other forms to the dorsiventral dictyostele. This explanation is a purely morphological one, and it raises at once the question as to possible causes of the arrested development in such examples. It seems worth while, therefore, to consider whether the Size Factor\* is not one of the underlying causal factors leading to the variations in stelar structure observed in the Vittarieæ. For this purpose measurements of the steles of the various forms examined were made, and these are given in the table below. The diameter of the stele is given in cms., the measurements having been made under a magnification of 28.

Name.	Diameter of Stele in cms. (Measurements obtained under Magnification of 28.)	Remarks.
<i>Hecistopteris pumila</i> . . .	0.15	Protostele with simple oval xylem mass.
<i>Monogramma graminea</i> . . .	0.4	Protostele with curved xylem mass.
<i>Monogramma trichoidea</i> . . .	0.4	Do.
<i>Monogramma paradoxa</i> . . .	0.4	Do.
<i>Antrophyum plantagineum</i> . . .	2.0	Medullated protostele, solenoxyllic.
<i>Vittaria elongata</i> . . .	2.2	Medullated protostele, dictyoxyllic.
<i>Antrophyum lanceolatum</i> . . .	2.5	Dorsiventral dictyostele.
<i>Antrophyum lineatum</i> . . .	2.5	Do.
<i>Vittaria lineata</i> . . .	3.0	Do.
<i>Antrophyum brasiliense</i> . . .	3.0	Do.
<i>Antrophyum reticulatum</i> . . .	4.0	Do.
<i>Anetium citrifolium</i> . . .	5.6	Perforated dorsiventral dictyostele.

The measurements given in the table indicate clearly that there is a correlation between the size and the complexity of the stele. The physiological significance of this correlation has already been fully discussed by the writers mentioned and therefore need not be entered into in this place. It has already been pointed out that the dorsiventral dictyostele is probably the central type of stele in the Vittarieæ, and that the anomalous steles of *Monogramma*, *Hecistopteris*, *Antrophyum plantagineum*, and *Vittaria elongata* are arrested developments. The interesting point is that all the anomalous steles mentioned are smaller than any of the dorsiventral dictyosteles. It may be concluded, then, that the arrest of the ontogenetic development at various stages, viz. the protostelic stage in *Monogramma* and *Hecistopteris* and the medullated condition in *A. plantagineum* and *V. elongata*† is due to, or at any rate is correlated with, a decrease in the size of the stele. On the other hand, the most complex type

\* For full discussions of the Size Factor the following should be consulted: BOWER, F. O., "Size, a neglected Factor in Stellar Morphology," *Proc. Roy. Soc. Edin.*, vol. xli; "The Relation of Size to the Elaboration of Form and Structure of the Vascular Tracts in Primitive Plants," *Proc. Roy. Soc. Edin.*, vol. xliii; WARDLAW, C. W., "Size in Relation to Internal Morphology," No. 1, *Trans. Roy. Soc. Edin.*, vol. liii; No. 2, *Trans. Roy. Soc. Edin.*, vol. liv.

† The dictyoxyllic stele of *V. elongata* is slightly larger than the solenoxyllic one of *A. plantagineum*, but it seems possible that the difference between these two is due to either an increase in the length of the leaf-gaps or the closer insertion of the leaves on the rhizome rather than to the operation of the Size Factor, for there is practically no difference between the ratios of surface to bulk in these two steles.

of stele found in the Vittarieæ, namely, that of *Anetium citrifolium*, may reasonably be regarded as due to an increase in the size of the stele, although it must be pointed out that the dictyostelic condition is already evident in quite young rhizomes with relatively small steles.

The tracheids of the xylem in all the forms examined are disposed in narrow bands, one, or at most two, tracheids in thickness. This arrangement ensures an adequate surface of contact between the tracheids and living parenchymatous cells, a fact which appears to be of considerable physiological importance.\* The small protosteles of *Monogramma* and *Hecistopteris* are of interest in this respect. That of *Hecistopteris* has very few tracheids and these are arranged in the form of an oval mass. In the rather larger steles of *Monogramma*, where the number of tracheids is greater, these latter are disposed in a narrow curved band, so that all the tracheids are still in contact with living cells. The form of the xylem mass in *Monogramma* differs from that in the protosteles of other Ferns where the tracheids usually form a cylindrical core, and the necessity for maintaining the xylem in contact with living cells is met by intermingling parenchyma with the tracheids.

#### THE ENDODERMIS.

The endodermis in all forms of the Vittarieæ examined is in the primary condition,† a condition which is unusual in the Filicales. Apart from the Vittarieæ it is only found in the Ophioglossaceæ, Marattiaceæ, in *Trichomanes*, and in certain "storage rhizomes" such as that of *Dryopteris Filix-mas*; elsewhere the endodermis is in a secondary condition. PRIESTLEY and RADCLIFFE (*loc. cit.*) have suggested that the primary condition of the endodermis in the forms they examined is to be correlated with the entirely parenchymatous nature of the cortex and medulla which is characteristic of these forms. They state in their conclusion that they are unable to suggest any reason for the failure of the endodermis to reach the secondary stage, but elsewhere they make the statement that "it seems more correct at present to consider the absence of the suberin lamella as responsible for the bulky, food-packed rhizome than the presence of these food supplies as responsible for the absence of the lamella."

In the Vittarieæ, as in the forms examined by PRIESTLEY and RADCLIFFE, the primary condition of the endodermis appears to be correlated with the entirely parenchymatous nature of the ground tissue. It is interesting to note that in the genus *Pleurogramma*, a genus similar in habit and habitat to *Monogramma*, though not related to it, the endodermis is secondary and the ground tissue practically entirely sclerenchymatous. It seems probable, then, that the nature of the endodermis and the histological nature of the ground tissue are bound together by some physiological tie, although the nature of this latter is entirely unknown.

The failure of the endodermis to reach the secondary stage may be bound up in some way with the reduction phenomena which have led to a decrease in the amount of phloem and xylem present in the steles of the Vittarieæ. The lack of data with regard to the physiology of such forms as the Vittarieæ precludes, however, any attempt to suggest any of the causal factors leading to this reduction.

#### TAXONOMY AND AFFINITIES OF THE VITTARIEÆ.

The first question for consideration is as to whether the Vittarieæ is a homogeneous group or not. The work of GOEBEL and BENEDICT and the facts detailed in this memoir indicate

\* See works already cited and "Some Points in the Anatomy of *Dicksonia*," S. WILLIAMS, *Proc. Roy. Soc. Edin.*, vol. xlv.

† PRIESTLEY and RADCLIFFE, "A Study of the Endodermis in the Filicineæ," *New Phyt.*, vol. xxiii. These writers distinguish between: (a) Primary Endodermis, with Casparian strip, and (b) Secondary Endodermis, with a suberin lamella.

that the grouping together of the genera *Vittaria*, *Monogramma* (limited to the *Eumono-*  
*gramme* section), *Antrophyum*, *Hecistopteris*, and *Anetium* is a very natural one. Evidence  
that this is so is afforded by a number of different characters:

(a) The anatomy of the five genera is based on a common plan. In all the species examined  
the endodermis is in the primary condition, and correlated with this is the fact that scler-  
enchyma is entirely absent. The most common type of stelar structure is the dorsiventral  
dictyostele; modifications of this type, which have already been discussed, are found in some  
of the genera.

(b) The sporangia in the five genera are all very similar, possessing, as they do, a four-  
celled stomium, an epi- and hypo-stomium each of two cells, and stalks which are always  
one-celled below but several-celled just below the capsule.

(c) They all possess clathrate scales. These are characteristic for each genus, but under-  
lying common features are present in all.

(d) They all possess spicule cells.

(e) All the fronds, except those of *Monogramma* and *Hecistopteris*, show a reticulate  
venation.

(f) The roots bear numerous brown root hairs, although this character is probably to be  
correlated with the epiphytic habit of the plants.

(g) The gametophyte generation, in such forms as have been examined, is divergent from  
the normal type, being deeply lobed and characterised by the occurrence of vegetative budding  
and the formation of gemmæ.

Although at the present time attempts to place even genera in phylogenetic relation with  
one another are viewed with suspicion, yet the present writer feels that it is worth while to  
endeavour to indicate the possible lines of development of the structural features character-  
ising the group of genera under consideration.

GOEBEL holds the view that *Antrophyum* represents the most primitive condition within  
the group, and that the other genera are derivative from this along a number of lines. The  
evidence advanced in support of this view does not appear to be conclusive, and it seems  
unlikely that *Antrophyum*, with its sporangia distributed over the whole leaf-surface, is a  
primitive form. It seems, indeed, far more probable that the structural features of *Vittaria*  
are the most primitive within the group. The anatomy, the character of the dermal append-  
ages, and the structure of the sporangia are all so constant in *Antrophyum* and *Vittaria* that  
they do not give much help in deciding which of these two genera is the more primitive. The  
arrangement of the sporangia in slightly intramarginal lines in *Vittaria* is, however, certainly  
more primitive than the sporangial arrangement in *Antrophyum*. Spore counts, while of  
proved value in the treatment of more primitive groups, are not so valuable in the considera-  
tion of such an advanced group as the Vittariæ. It is, however, the case that *Vittaria* has  
the largest number of spores per sporangium, viz. 64, and this fact supports the view that  
*Vittaria* is relatively primitive. Moreover, *Vittaria* appears to offer a more favourable oppor-  
tunity of linking the Vittariæ with other groups of genera.

*Monogramma* appears to be closely related to *Vittaria*, and it is probable that GOEBEL's  
view that the structure of *Monogramma* has been arrived at by an arrest of the development  
of *Vittaria* characters is correct. *M. paradoxa* offers the closest link, particularly if the draw-  
ings of BENEDICT of the venation of large fronds be correct. In these latter there is a practically  
typical *Vittaria*-like venation and soral arrangement. In smaller fronds there has been  
an arrest of the ontogeny and the venation is simpler, showing a sympodial dichotomous  
scheme similar in essentials to that present in the fronds of young plants of *Vittaria*. *M.*



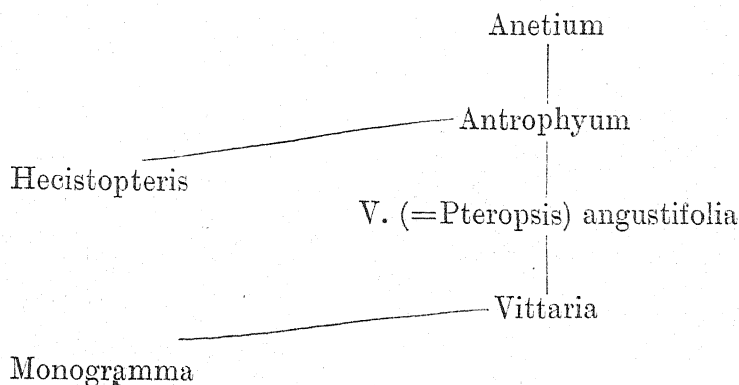
*graminea* appears to offer the last stage of arrested development and the frond has only the mid-rib present, *i.e.* the same structure as the first-formed fronds of the seedlings of *Vittaria* species. It has also been pointed out in the discussion of stelar problems that the steles of *Monogramma* species may be regarded as arrested developments of the dorsiventral dictyostelic type of structure which is characteristic of *Vittaria* species.

An advance upon the condition of such forms as *V. lineata* and *V. elongata* in the direction of a more complex venation is offered by *V. (=Pteropsis) angustifolia*, where, although the sporangia are still arranged in slightly intramarginal lines, there are several rows of meshes on each side of the mid-rib and, where the marginal areolæ are small, the sporangial groove may extend over the whole of the mesh. This condition leads on very naturally to the structure of *Antrophyum* with its characteristic reticulate venation of several rows of areolæ and the distribution of the sporangia along the vertical veins of the meshes. Several points indicate that the characters of the section of *Antrophyum* with the sporangia immersed in grooves are more primitive than those of the section with the sporangia borne superficially on the surface of the frond. For instance, spore counts obtained from species in the latter section indicate that the typical spore output per sporangium is smaller than that of species in the former section. Another point is that the stelar construction of such a form as *A. brasilianum* is more complicated than any seen in species of the first section. Finally, the condition of having the sporangia naked on the surface of the frond may, on general grounds, be regarded as derivative from the protected condition.

The sporangial distribution characteristic of *A. brasilianum* and other species in the same section leads on naturally to the acrostichoid condition of *Anetium citrifolium*. This latter stands considerably apart from the rest of the Vittariæ and is certainly a very advanced form. The nature of the dermal appendages, the structure of the sporangia, and the presence of spicule cells are all points of resemblance to the other genera of the Vittariæ. It is in the sporangial distribution and stelar morphology that the genus shows a considerable divergence from the other forms. The presence of sporangia not only on the veins but also on the parenchyma of the areolæ is a marked advance on the condition, say, of *A. brasilianum*. The stele of *Anetium* is also much more complex than that of any other genus. Finally, its advanced position is indicated by the small spore output per sporangium (32 or 48).

There remains only to be considered the position of *Hecistopteris*. GOEBEL has put forward the view that the curious features of this genus are the result of an arrest of the development of the structures characteristic for *Antrophyum*, and the facts seem to justify this view. The open dichotomous venation may reasonably be held to be due to the arrest of the development of the reticulate venation of other genera since the fronds of young plants of *Antrophyum* and *Anetium* show a similar type of venation. The forked outline of the leaf itself offers rather more difficulty, but this is at least partially removed by a consideration of the fact that seedling leaves of *Antrophyum* are sometimes not simple in outline but dichotomously branched following the outline of the venation. One point against the view that *Hecistopteris* is allied to *Antrophyum* is that the clathrate scales of the former more nearly resemble those of *Vittaria* than they do those of *Antrophyum*, for they have no unicellular outgrowths from the basal cells such as the scales of the latter genus exhibit.

The suggested relationships between the five genera of the Vittariæ may be expressed diagrammatically as follows:—



The conclusions reached above with regard to the relationships of the genera of the Vittarieæ confirm DIELS's arrangement of this group in the *Pflanzenfamilien*. This writer divides the group into the Vittariinæ including *Monogramma* and *Vittaria*, and the Antrophyinæ including *Hecistopteris*, *Antrophyum*, and *Anetium*. The only criticism of this arrangement is as to whether it would not be better to remove *Anetium* from the Antrophyinæ and place it in a separate section on account of its anomalous and advanced structural features. The present arrangement is, however, sound in that it indicates the affinity of *Anetium* with *Antrophyum*.

The relation of the genera to one another above outlined seems fairly clear and justified by the facts. It is, however, a matter of considerable difficulty to make any definite statement about the phyletic relation of the Vittarieæ as a whole with other and more primitive forms, and any such statement would certainly be open to the criticisms which have been levelled against phyletic morphology in general during recent years. Nevertheless, the data now available concerning the Vittarieæ seem to justify tentative suggestions being made as to the affinities of this group. Such suggestions must, however, be regarded as a contribution to a natural classification of the Ferns under consideration and not as an attempt to link phyletically any forms now living.

BENEDICT has suggested that the Vittarieæ are related to the Pterideæ and Aspleneæ, basing his conclusions on the nature of the scales and sporangial arrangement. This view does not seem to be based on a sufficiently broad consideration of the characters which have been proved to be useful in endeavours to build up a natural classification, and the present writer finds himself unable to support this view. A broader consideration of the question of the affinities of the Vittarieæ will now be made on the basis of an examination of a number of characters which have been shown to be important in making systematic comparisons.

(a) *Arrangement of Vascular Tissue*.—The very frequent occurrence of dorsiventral dictyosteles and steles related to this type in the Vittarieæ leads to an inquiry as to the prevalence of this type of stelar structure in other genera. A consideration of this point shows that such steles are most common in such genera as *Adiantum*, *Gymnogramme*, *Cheilanthes*, and *Pellaea* (see GWYNNE-VAUGHAN, *loc. cit.*, and MARSH, *Ann. Bot.*, 1914), a group of genera which Professor BOWER has already shown to form a natural and homogeneous group. It is also noteworthy that the anomalous type of dorsiventral dictyostele found in some mature rhizomes of *Antrophyum reticulatum* finds a very close parallel in the stelar structure of *Cheilanthes lendigera*. Two other points in the anatomical construction of *Pellaea* and *Cheilanthes* may be mentioned. In neither *Pellaea* nor *Cheilanthes* is any protoxylem distinguishable; this also holds for all the Vittarieæ examined. Secondly, in the species examined by

MARSH, the phloem always consists of small elements corresponding to the protophloem of other Ferns; the nature of the phloem in all the Vittarieæ examined is comparable to this.

(b) *Spicule Cells*.—The presence of spicule cells has proved to be a very constant feature of the Vittarieæ. The only other genus in which such structures have been recorded is *Adiantum*. POIRAULT (*loc. cit.*, p. 208) gives a detailed account of their occurrence in a large number of the species of this genus. The appearance of the spicule cells in such species of *Adiantum* as I have examined is very similar to that of the spicule cells of the Vittarieæ.

(c) *Clathrate Scales*.—Scales of very similar appearance to those of the Vittarieæ are present in *Adiantum macrophyllum*, but the data with respect to this character are very scanty. It must be noted, however, that BENEDICT found clathrate scales present in the Pterideæ and Aspleneæ, though he does not state in which genera they occur.

(d) *Venation*.—Reticulate venation is a character which has been developed in a number of circles of affinity, and it is therefore a character which is not of much value for tracing relationships. The venation of the fronds of young Fern plants is always based on a dichotomous plan, so that it also is not usually a very good guide to affinity. The Vittarieæ, however, are almost unique in so far as the first-formed frond is single-veined in all the genera, with the possible exception of *Anetium*. So far as I am aware the only other genus which possesses a single-veined cotyledon is *Ceratopteris*. Indeed, the whole ontogeny of the frond of the latter genus resembles very closely that of some of the Vittarieæ.

(e) *Sporangia*.—The structure of the sporangium of advanced Ferns is relatively constant, and accordingly is not a very good character for comparative purposes when dealing with such advanced types as the Vittarieæ. It may be noted, however, that the sporangia of *Adiantum* species, e.g. *A. polyphyllum*, and of species of *Pellaea*, e.g. *P. cordata*, are similar to those of the Vittarieæ in having a four-celled stomium. The marked and apparently characteristic instability of the characters of the annulus and stomium of *Cheilanthes*, *Gymnogramme*, *Pellaea*, and *Ceratopteris* does not, however, find any parallel in the Vittarieæ. The sporangia of the latter are very constant in their characters.

The structure of the stalk of the sporangia of the Vittarieæ seems constant, with small variations, within the group. The curious dilation of the stalk immediately below the capsule may, however, be directly correlated with the protection of the sporangia in deep grooves and the consequent necessity for a special mechanism to ensure the successful scattering of the spores. That this is so is indicated by the fact that the dilation is greatest in those species with deep sporangial grooves, and least marked in those where the sporangia are superficial. If this direct correlation exists, it is unlikely that the stalk characters will be of much use in tracing affinities in the group under consideration.

(f) *Arrangement of Sporangia*.—The examination of the ontogenetic development of the sorus of *V. lineata* above described indicates that the origin of the sorus is slightly intramarginal. In this respect it resembles *Cheilanthes* and *Ceratopteris* and differs from the Pteroid series.

Taken in conjunction, the above points of contact between the Vittarieæ and the group of genera including *Adiantum*, *Cheilanthes*, *Pellaea*, and *Ceratopteris* may be held to point to an affinity between the former and the latter. Some of the points, such as the presence of spicule cells and clathrate scales are admittedly small, but when they run parallel with more important characters such as the stelar construction and the origin of the sorus, they may reasonably be regarded as being of some value for comparative purposes. It seems probable that the condition of *Adiantum* presents the nearest point of contact with the Vittarieæ, but, on the facts available, there seems no good ground for assuming that there is any direct



phyletic connection between them. The soundest conclusion appears to be that the Vittarieæ must be placed in any natural classification along with the complex of genera containing *Adiantum*, *Gymnogramme*, *Cheilanthes*, *Pellæa*, and possibly *Ceratopteris*. It does not fall to the present writer to discuss the origin of this complex since this has already been dealt with by Professor BOWER.

## SUMMARY.

1. The genera *Vittaria*, *Monogramma*, *Antrophyum*, *Hecistopteris*, and *Anetium* have been examined with regard to a number of characters, and it is concluded that they form a homogeneous group.

2. Suggestions are made as to the inter-relationships of these genera.

3. It is further suggested that the Vittarieæ must be placed in any natural classification along with the Gymnogrammoid group of Ferns.

4. With regard to the vascular structure it is concluded that the dorsiventral dictyostele is the central type of stelar construction in the group. Certain deviations from this type, hitherto regarded as being reduced, are shown to be arrested developments. This arrest of the normal ontogenetic development is correlated with decreases in the size of the stele.

5. The endodermis is always in the primary condition, and this fact is correlated with the entirely parenchymatous nature of the ground tissue.

In conclusion, I desire to express my thanks to the Executive Committee of the Carnegie Trust for a grant to defray the expense of the illustrations of this memoir.

## DESCRIPTION OF PLATES.

## PLATE I.

(Photographs of herbarium specimens by Mr D. M. FILSHILL.)

- A. *Vittaria lineata*.
- B. *Vittaria elongata*.
- C. *Monogramma paradoxa*.
- D. *Monogramma graminea*.
- E. *Hecistopteris pumila*.

## PLATE II.

(Photographs of herbarium specimens by Mr D. M. FILSHILL.)

- A. *Antrophyum reticulatum*.
- B. *Antrophyum plantagineum*.
- C. *Antrophyum lineatum*.
- D. *Anetium citrifolium*.

## PLATE III.

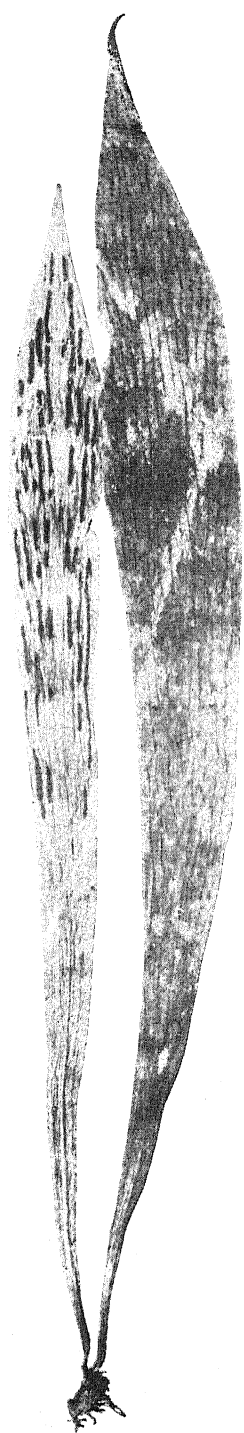
- A. Model of dorsiventral dictyostele of *Antrophyum lineatum*, showing two closely inserted nodes.
- B. Model of node and internode of *Anetium citrifolium*.
- C, D, and E. The stele of a seedling plant of *Antrophyum reticulatum* at different levels in the rhizome (description in text).  $\times 110$ .



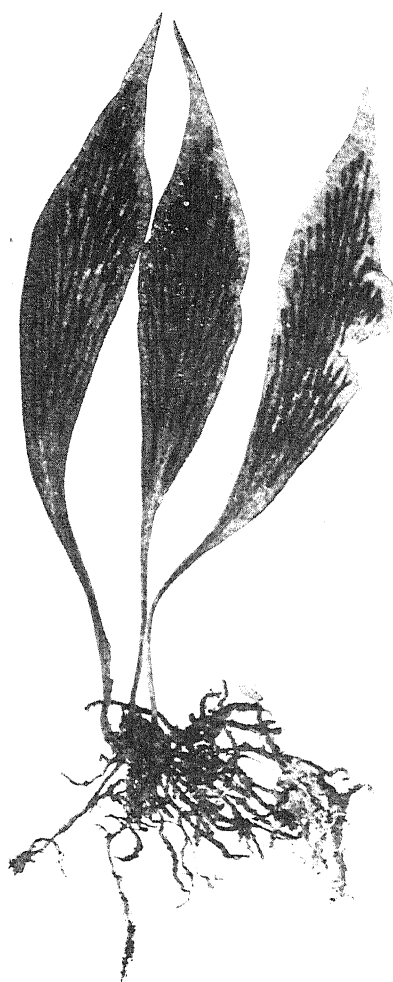








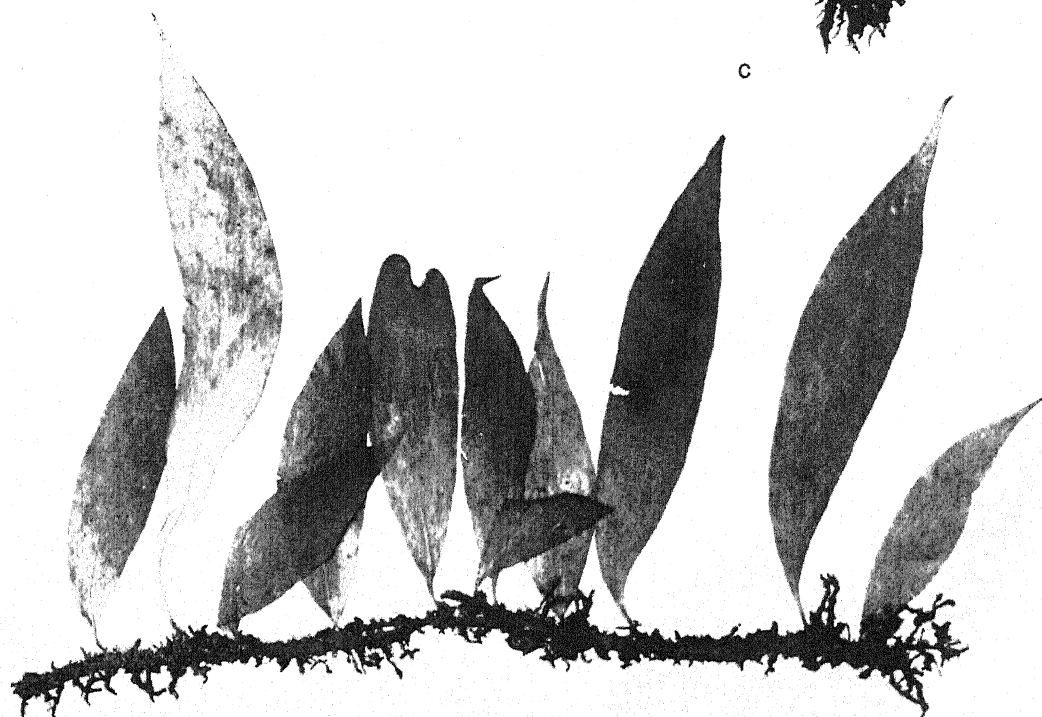
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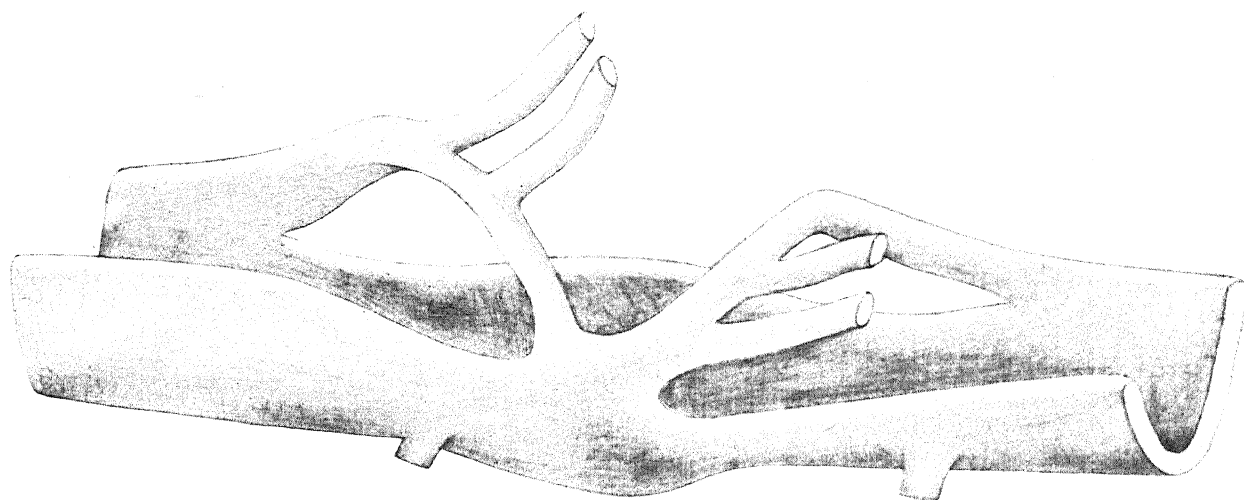
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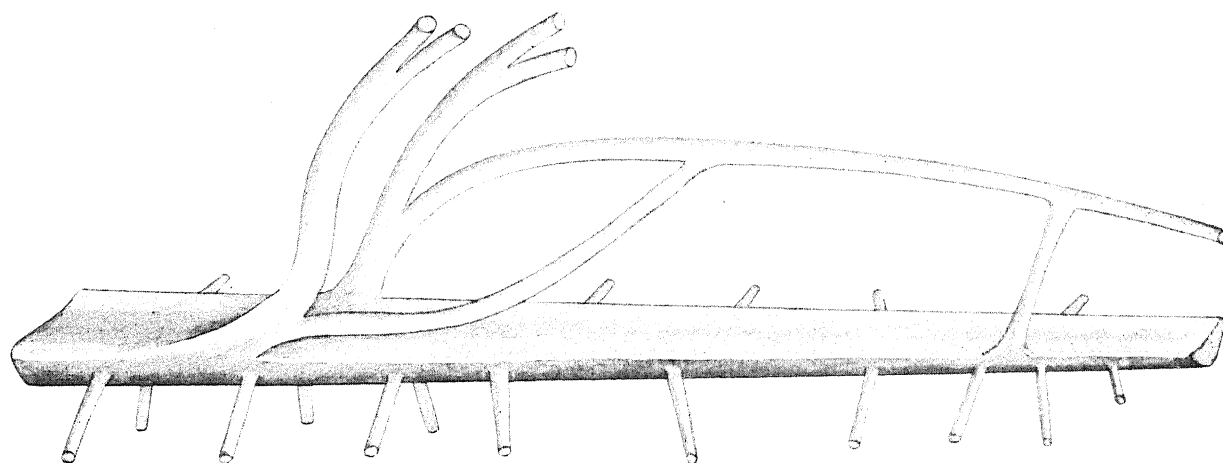
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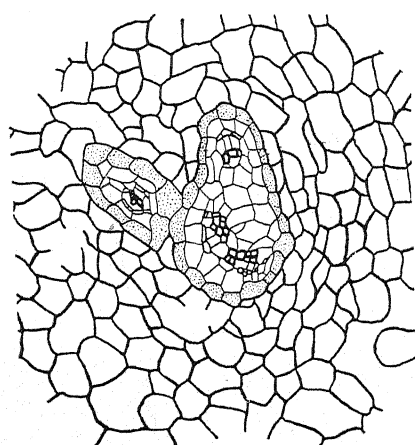




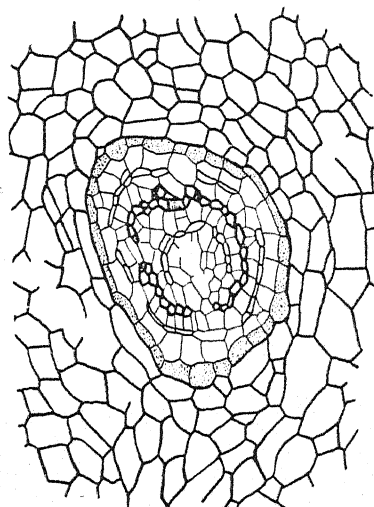
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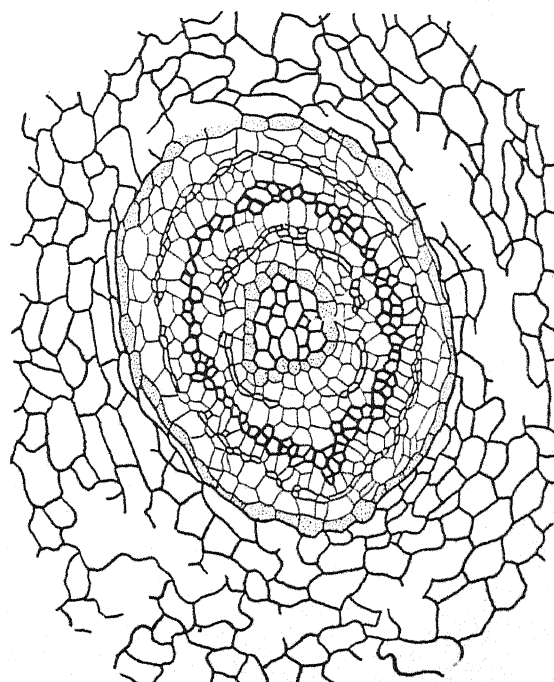
B



C



D



E



X.—On the Feeding Mechanism of a Mysid Crustacean, *Hemimysis lamornæ*. (From the Zoological Department of the Imperial College of Science and Technology, South Kensington, London.) By H. Graham Cannon, M.A., D.Sc., F.L.S., Professor of Zoology in the University of Sheffield, and Miss S. M. Manton, B.A., Yarrow Student of Girton College, Cambridge. Communicated by Professor J. H. Ashworth, F.R.S. (With Four Plates and Sixteen Text-figures.)

(MS. received October 6, 1926. Read December 6, 1926. Issued separately March 4, 1927.)

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#### INTRODUCTION.

The general biology of the Mysids has recently been studied at great length by BLEGVAD (1922) at Copenhagen. His paper, containing a very complete literature list, deals with *Mysis inermis*, Rathke, *Mysis flexuosa*, Müller, and *Mysis neglecta*, Sars. His comments on feeding are limited, and refer chiefly to the nature of the food that the animals ate in captivity. GELDERD's work (1909) on the digestive system of the Schizopoda describes the course taken by the food through the gastric mill, the masticatory functions of this apparatus, and the method by which the masticated food and digestive juices are brought together, but does not deal with the manner in which the food reaches the stomach. An account, then, of the method by which a mysid collects its food would fill a gap in our knowledge of these forms. The only description, as far as we are aware, of the feeding habits of a mysid is that of DEPDOLLA (1923), who worked on *Praunus [Mysis] flexuosus*, but his account is superficial and in our opinion very inaccurate. The following paper deals with the feeding habits of a small mysid, *Hemimysis lamornæ*, about 8 mm. long, which has established itself in the larger fish-tanks at the M.B.A. laboratory at Plymouth. It breeds freely all the year round, and can be obtained from the tanks in abundance, although it is stated to be only a rare visitor in the Plymouth district.

#### METHODS.

*Hemimysis*, besides feeding on large masses of food, filters a portion of the currents produced by its thoracic limbs and eats the particles so collected. Observations on the general movements of the animal, and the currents it produces in the surrounding water, were made in small tanks, a carmine suspension being used to demonstrate the currents. In order to watch more closely the movements of the limbs and the course of the currents close to the body, single individuals were confined in water in a narrow space between two vertical glass plates.

The finer movements of the mouth-parts were observed by the aid of the microscope. Individuals with chromatophores contracted and with empty stomachs were chosen for this purpose because of their greater transparency. The animals can be induced to lie on their backs in a small volume of water in a watch-glass. They feed readily in this position, and all



the limb movements appear to be carried out normally. Large pieces of food, such as a *Sagitta*, are taken and eaten as readily in this position as by freely swimming individuals. The feeding currents formed by the constant activity of the limbs, and the course taken by suspended particles in the surrounding water to the mouth, can be followed. Suspensions of carmine, carborundum powder, charcoal, mud, *Nitzschia*, and starch were used. A fine starch stained with iodine is the most efficient, because the grains do not stick to the limbs and setæ, and thus do not clog the feeding mechanism as does carmine or an excess of mud. Each grain remains separate, and can be seen clearly, owing to its blue colour. The starch, moreover, appears to be palatable and is not rejected as is charcoal. *Nitzschia*, also, is readily eaten, but the individual diatoms cannot be seen clearly enough to follow their exact path to the mouth.

Animals kept in a suspension of iron saccharate automatically collect the granules and pass them on to the mouth and remain apparently perfectly healthy. The saccharate must be somewhat sticky, as it remains on the filtering combs of setæ and in the food groove even after sectioning. The particles are clearly visible in sections of animals killed and subsequently treated with potassium ferrocyanide. By this means the parts of the limbs responsible for filtering the food stream, and the distribution of the food matter in the groove, can be seen in serial sections and compared with conclusions drawn from direct observations.

The detailed arrangement of the limbs was ascertained from dissections cleared in glycerine. Animals for this purpose were fixed in hot alcohol and in corrosive sublimate. All the figures were drawn from such dissections.

#### TOPOGRAPHY OF MOUTH-PARTS.

As a preliminary, a somewhat detailed description must be given of the mouth-parts and trunk limbs and of their topographical relations to one another. The organs directly concerned with putting food into the mouth are the mandibles, together with the labrum and paragnaths, the maxillules and maxillæ, and the bases of the first trunk limbs. The eight pairs of thoracic appendages cause food to be brought from a distance to the mouth-parts. The general disposition of the limbs can be seen from the ventral, lateral, and internal sagittal views (figs. 1, 2, 5, text-fig. 3).

The entrance to the mouth is situated at the ventral side of the head, and is bounded anteriorly by the large ventrally projecting labrum, and posteriorly by a pair of laterally placed, but similarly ventrally projecting, paragnaths. The entrance leads into an oral cavity shaped like an inverted L. The long arm points vertically upwards and may be termed the lower oral cavity. The short arm points horizontally forwards and is called the upper oral cavity. The lateral walls of the upper oral cavity are formed by the biting surfaces of molar processes of the mandibles. Its floor (morphologically the anterior wall) is formed from the posterior face of the labrum, and this curves upwards in front of the molar processes to the commencement of the œsophagus. The roof is formed by the ventral median ectoderm immediately behind the œsophagus. The lower oral cavity is bounded anteriorly by the posterior face of the labrum; and at its upper limit, where it bends round to form the floor of the upper oral cavity, a median muscle is attached which runs to the anterior labral ectoderm. Other paired labral muscles are inserted laterally in the floor of the upper oral cavity and traverse the labrum in various directions. The lateral walls of the lower oral cavity are formed by the incisor processes and *lacinix mobiles*, the spine-rows of the mandibles occupying the angle between the upper and lower oral cavities. The lower oral cavity has no posterior wall, but this space is occupied by a vertical split between the two downwardly projecting

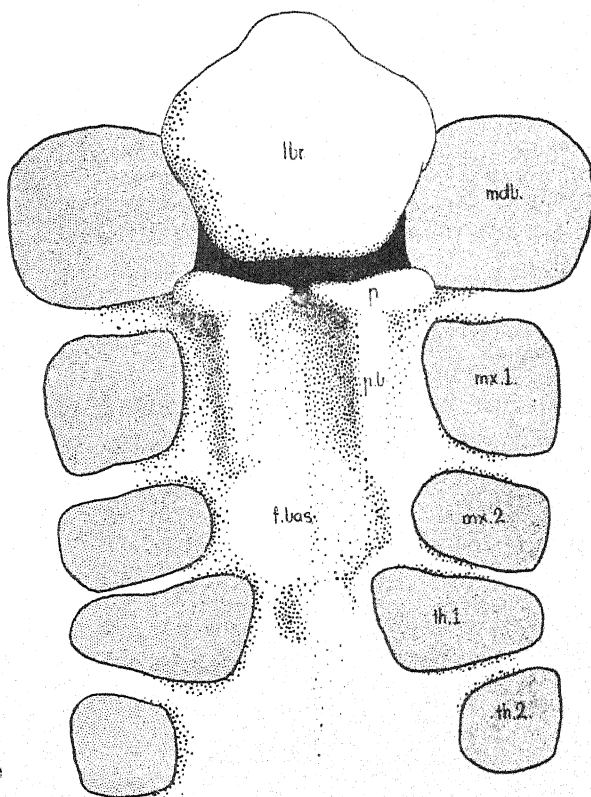
paragnaths. Thus the actual mouth—that is, the space through which food passes on its way to the œsophagus—is not limited to the space bounded by the tips of the upper and lower lips, but extends dorsally between the latter. Hence, food may pass in between the upper and lower lips directly on to the incisor processes of the mandibles, but also it may pass directly from behind between the two paragnaths on to the spine-rows or even directly on to the molar processes.

The tips of the paragnaths are flattened in a transverse plane, and laterally wrap closely against the outer surface of the mandibles, extending forwards almost to meet the lateral portions of the labrum which similarly lie close against the mandibles (figs. 2 and 5, text-fig. 1). Their bases form a pair of broad ridges extending posteriorly. The paragnaths have in side-view the form of a right-angled triangle, the hypotenuse extending from the tip to the anterior limit of the maxillary segment. There is thus formed between them a deep channel. This expands posteriorly immediately beyond the paragnaths into a wide depression that we term the “food basin,” bounded laterally by the bases of the maxillæ. Posteriorly it is limited, at the sides, by the bases of the first trunk limbs, while in the middle line the ectoderm is slightly raised. The food basin is continuous in this region, with a median food groove extending posteriorly between the thoracic limbs to the limit of the trunk. Behind the first thoracic limbs this groove widens considerably (fig. 1 and text-fig. 1). The ventral edges and median internal faces of the paragnaths are provided with fine hairs, and the internal anterior edges close to the mandibles are densely clothed with hairs and stronger setæ.

The chief component of the endoskeleton is a horizontal V-shaped plate lying above the nerve cord (fig. 2a and text-figs. 2b and 2c). The apex of the “V” is directed forwards and is attached to the mandibular tendon in the

middle line. Posteriorly, the arms are continuous with the lateral exoskeleton in the posterior part of the maxillulary segment. The whole plate is hollow, the internal cavity being open to the exterior posteriorly. From the posterior arms of the plate a pair of blind tubes extends through the maxillary segment to a tendon between the maxillary adductor muscles. To this endoskeleton are attached muscles to the maxillæ, maxillules, and stomach, and also a median muscle to the deep food groove between the paragnaths.

The mandibles exhibit well-developed spine-rows and *lacinie mobiles*, and are provided with large palps (figs. 1, 2, and 5). The labrum extends just below the anterior edges of the incisor processes, and laterally reaches the bases of the mandibular palps. The palps are two-jointed, the basal joints are wide and flattened and fit closely round the labrum, nearly



TEXT-FIG. 1.—Ventral view of the oral region with appendages removed, showing the ventral food groove and the food basin and the positions of the labrum and paragnaths.

f. bas., food basin; lbr., labrum; mdb., mandible; mx. 1, maxillule; mx. 2, maxilla; p., paragnath; p. b., paragnath base; th. 1, first thoracic limb; th. 2, second thoracic limb.





meeting one another anteriorly in the middle line. Setæ project from both inner and outer edges, those on the inner side partially closing the small gap between the two palps and between the palps and labrum. The distal joint of the palp is not markedly flattened. From its inner side project a few simple setæ which are usually found interlocked with those from the other side. Stout, feathered setæ spring from the outer side ventro-laterally and from the tip. The proximal setæ are long and sharply pointed, while those of the distal half of the row are shorter and blunt, with stout lateral spines. The row becomes inserted more ventrally towards the tip of the palp. At the tip stands one long seta curving outwards and slightly backwards, and provided with strong, lateral spines and also a lateral row of eight short-hooked spines with fine lateral feathering (fig. 5).

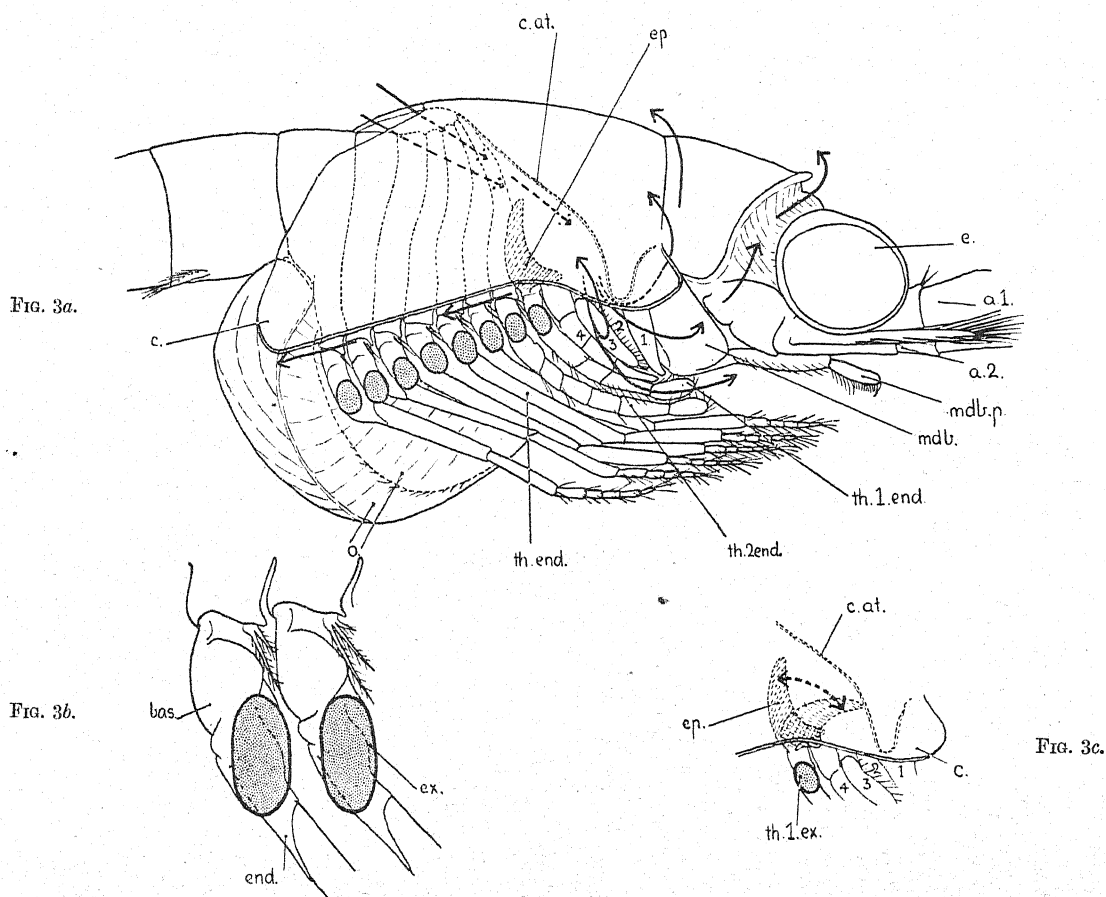
The biting edges of the mandibles are asymmetrical, as also is the posterior edge of the labrum (fig. 3). The biting edge of the left mandible is, as a whole, more ventral than the right. Its *lacinia mobilis* is large and biting, equalling in size its incisor process. The spine-row consists of about five adorally curved spines, each inserted separately on the mandible and bearing strong lateral spines along the convex ventral edge. The incisor process of the right mandible bites against the incisor process and *lacinia mobilis* of the left side, its longest point extending between these two biting parts. The right *lacinia mobilis* is smaller than the left and is of quite a different shape. Its inner surface bears two horizontal rows of spines which increase in size posteriorly. The rows converge towards a large, single spine at the anterior inner edge. The hollow between the rows is ridged. As the mandibles close, the left spine-row slides over the spines of the right *lacinia mobilis*, and comes to rest against the large anterior spine of the latter. The right spine-row is situated opposite the gap between the left spine-row and molar process. All the spines are straight, with lateral spikes along both edges. The most ventral spine is inserted separately on the mandible; and the remaining spines, about seven in number, are united together by the bases giving one insertion for the group. The *lacinia mobilis* on each side and the various parts of the spine-rows are probably all passively movable, with the possible exception of the ventral separated spine on the right mandible, which appears to be rigid. The right molar process extends higher up than the left, and the ridges on the grinding surfaces on each side are not identical. Each molar process is tipped with a bunch of setæ, the group being larger on the left mandible.

The edge of the labrum shows a thickened ridge in the region of the incisor processes, the thickening being greatest over the right mandible (fig. 3a). On the right side it is covered with a paving of short cylindrical denticles closely packed together. On the left side their place is taken by longer, overlapping spines, which are much flattened with serrated edges. Sparse hairs cover the posterior face of the labrum chiefly in the middle line. At the junction between the upper and lower oral cavities stands a median group of strong setæ (figs. 2 and 4, *sp. f.*). These are inserted partly on the projecting ridge dividing the two oral cavities and partly on the floor of the upper oral cavity. They are thus situated opposite the space between the spine-rows and molar processes.

The maxillules lie close against the paragnaths (figs. 2, 4, and 5, and text-fig. 2b). The distal endites form powerful biting jaws at the ventral extremities of the paragnaths and mandibles. They bear at their tips three rows of blunt, biting spines and a short row of setæ on the posterior face. The proximal endite is a small, rounded plate slightly overlapping the edge of the distal endite and more widely separated from its fellow in the middle line. The tip of this endite with its marginal setæ occupies the space between the distal endite and the ridge formed by the prolonged base of the paragnath (fig. 4). At their tips these endites each carry three very long, strong setæ which pass directly inwards, and with their feathered tips

curl round the edges of the paragnaths and point towards the mouth. These setæ meet in the middle line. From the upper edge of the first endite a single, long seta extends backwards to the base of the maxilla, lying outside the backwardly projecting ridge from the base of the paragnath.

The maxilla is inserted at a little distance from the maxillule but close to the first thoracic



TEXT-FIG. 3.—Lateral view of the thorax of a female, showing the arrangement of the limbs and carapace, the exopodites having been removed.

FIG. 3a.—Complete lateral view; the mouth-parts visible behind the mandible (*mdb.*) are in order from before backwards—the paragnath (1), the maxillule (2), the maxillary exite (3), the axis of the maxilla (4), and the first thoracic endopodite (*th. 1 end.*). The epipodite from the first thoracic limb extends under the carapace; the openings to the food groove lie between the basipodites (see fig. 3b). The course of the respiratory current is indicated and also a backward current between the basipodites and the edge of the carapace.  $\times 27$ .

FIG. 3b.—Enlarged view of the bases of the second and third thoracic limbs, to show the feathered setæ from the basipodites extending across the entrance to the food groove.

FIG. 3c.—Diagram showing the movements of the epipodite in the respiratory chamber.

a. 1, antennule; a. 2, antenna; *bas.*, basipodite; *c.*, carapace; *c. at.*, carapace attachment to the body; *e.*, eye; *end.*, endopodite; *ep.*, epipodite of first thoracic limb; *ex.*, exopodite; *mdb.*, mandible; *mdb. p.*, mandibular palp; *o.*, oostegites; *th. 1 end.*, first thoracic endopodite; *th. 1 ex.*, first thoracic exopodite; *th. 2 end.*, second thoracic endopodite; *th. end.*, endopodites of third to eighth thoracic limbs; 1, paragnath; 2, maxillule; 3, maxillary exite; 4, axis of maxilla.

limb (figs. 2b, 5, and text-fig. 2c). As a whole, it forms a curved plate lying anteriorly under the maxillule. On the inner side it curves upwards towards the food groove and on the outer also upwards overlying the side and base of the maxillule. The endites and palp are strongly fringed with feathered setæ. The first endite projects upwards and forwards into the food basin, bearing a comb of very finely feathered setæ forming a filtering plate. Its proximal

part bears one especially long-feathered seta which extends forwards and upwards, and reaches the three long setæ from the maxillule between the paragnaths. The distal joint of the palp forms with its setæ a flat plate, concave dorsally, lying immediately ventral to the maxillule and paragnath. The exite of the maxilla (text-fig. 3 and fig. 5) spans the space between the axis of the limb, the lateral body wall, and the maxillule, and so closes laterally the food space enclosed by the mouth-parts.

All eight pairs of thoracic limbs bear swimming exopodites (fig. 1 and text-fig. 3). The last six pairs of endopodites are similar, but the first two are specialised for feeding. All extend forwards to the mouth region. The endopodites of the first pair lie close below and slightly to the side of the maxillæ, and those of the second lie similarly, just below those of the first. The distal parts of the remaining endopodites stand further from the body and form a basket round and below the mouth-parts (text-figs. 3 and 9).

The first trunk-leg bears endites on the basipodite, ischiopodite, and meropodite, that on the basipodite being the largest.\* The proximal endite curves upwards into the food basin, and projects forwards below and inside the maxilla (figs. 1 and 2*a*). All three endites bear strong marginal setæ directed towards the mouth, and a few setæ springing from the lower inner edges pointing mainly inwards towards the middle line. These latter form a longitudinal row of stout, branched spines across the basal endite. They project inwards and downwards, meeting those from the opposite side, and thus form the floor of a space between these endites (text-fig. 2*c*). This space forms in effect a tube extending between the bases of the first trunk limbs to the paragnaths and so to the mouth. The endopodite is comparatively stout and short. The propodite is not multiarticulate, and the rounded dactylopodite is directed transversely towards the incisor process of the mandible, and is armed with claw-like spines and setæ.

The second pair of thoracic legs resembles the first, but bears no endites. The remaining endopodites have the propodite subdivided into four joints. The second to eighth limbs have the basipodites expanded into flat, triangular plates extending towards the middle line (fig. 1). From their point of origin the endopodites slope forwards and with them these inner plates of the basipodites. The latter thus overlap one another from behind forwards. From their inner edges a few groups of feathered setæ project, which may meet those from the other side of the body. Thus the basipodites and their inwardly directed setæ enclose a horizontal space between the limb bases and the ventral body wall, which is the food groove (text-fig. 2*d*). In the male the seventh and eighth endopodites are sometimes carried horizontally just below the gap between the more anterior basipodites, thus closing it. In the female this space is divided posteriorly into two lateral channels by the presence of the oostegites. The flanges of the basipodites fit closely against the latter, and the eighth endopodites may lie under the junction between the oostegites and basipodites. Narrow channels between the limb bases on each side put the lateral water in communication with the food groove. The outer ends of these channels are guarded by long-feathered setæ arising from the upper anterior edges of the basipodites, two from the third to eighth limbs, and three from the second (text-fig. 3). The tips of these setæ touch the basipodites of the next anterior legs. In the male the two penes stand in a vertical position close together between the last pair of trunk limbs, so leaving lateral spaces between each penis and the limb base (text-fig. 2*e*). Laterally the penes bear five long spines which lie across these openings and touch the eighth basipodites. In the female the equivalent openings lie between the eighth basipodites and the oostegites. The oostegites expand laterally behind the trunk limbs, and so these openings become lateral and

\* In this account we have used Dr CALMAN's terminology of the limb segments in Lankester's *Treatise on Zoology*, pt. 7, "Crustacea," London, 1909.



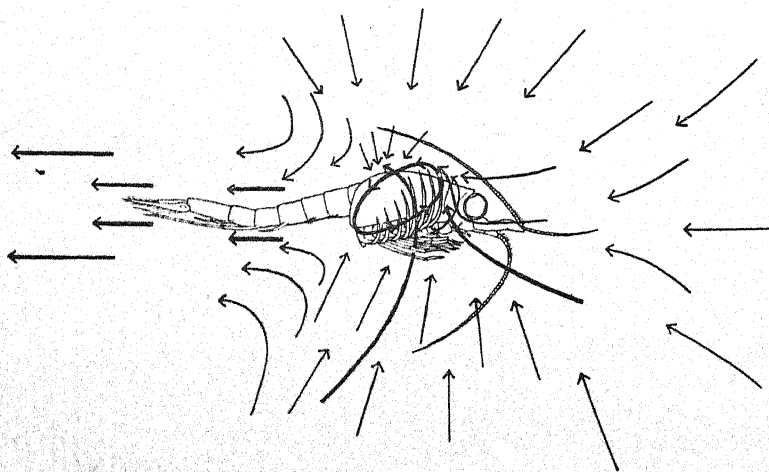
not posterior, as in the male (text-fig. 3). The openings in the female are not guarded by spines, but the eighth limb can be held down closely against the oostegite, so obliterating the passage.

The exopodites of all the thoracic limbs bear long-feathered setæ from the junctions between the joints (fig. 1 and text-fig. 6c). They stand in two rows, one pair from each joint, on the upper side of the axis. The setæ of the posterior row in the middle of the limb are smaller than those of the anterior row, and are absent from the first few segments. Two similar setæ are inserted on the end of the terminal joint. All these setæ lie close together, one outside the other, at the sides of the axis, and curve upwards distally. The axis of each exopodite with its setæ thus forms a spoon-shaped organ, concave dorsally. The anterior edge of this spoon is stronger than the posterior edge, being formed by the stouter proximal setæ of the anterior row.

The general shape of the thorax and carapace can be seen from text-fig. 3. Mid-dorsally the carapace is cleft posteriorly nearly to its attachment to the body over the second thoracic segment. The line of attachment of the carapace descends steeply to the maxillary region and rises again above the outer attachment of the mandibular muscle. Thus a space is present between the carapace fold and the body, which may be termed the respiratory chamber. Into it projects the single epipodite which is borne on the first trunk limb. Behind the first thoracic segment the body wall is grooved intersegmentally, but anteriorly such grooves are absent and the body wall is flat. The epipodite beats in a parasagittal plane over this region of the body. The epipodite is slightly concave anteriorly, and fits closely against the lateral walls of the respiratory chamber. In its forward position it almost touches the anterior wall formed by the carapace attachment, which in this region is somewhat hollowed-out anteriorly (text-fig. 3c).

#### SWIMMING AND FEEDING CURRENTS.

Hemimysis is usually found swimming in a horizontal position. Such locomotion is caused entirely by the movements of the thoracic exopodites. By their activity powerful currents are set up in the surrounding water, resulting in a forward movement of the animal.



TEXT-FIG. 4.—Lateral view of animal swimming freely, showing the currents produced in the surrounding water. The strongest currents lie outside the plane of the paper and are indicated by stouter arrows. One single lateral swirl is indicated. This is really composed of eight separate swirls, each produced by one exopodite.  $\times 6$ .

A portion of the water producing these currents is filtered, the minute organisms or suspended particles of detritus being retained and passed on to the mouth. Thus the exopodites are responsible for locomotion and at the same time for the production of the feeding current.

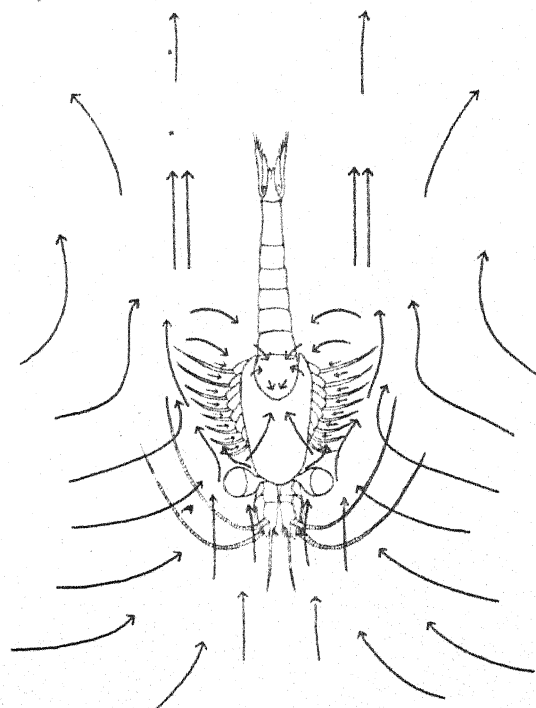
Water streams towards the thoracic region of the body from in front and from all sides (text-figs. 4 and 5). These streams are drawn up towards the dorsal level of the body, where they turn posteriorly, forming a pair of strong outgoing currents along the sides of the abdomen at a little distance from it. These two streams are more powerful than any others existing round the animal. They are of limited cross-section compared with the general drift of water

flowing towards the body from other directions, and they can be clearly seen for some distance behind the animal. They are of such strength that posteriorly they draw in some of the water drifting towards the thorax (text-fig. 5). These two outgoing currents represent the motive force which results in the forward movement of the animal.

The thoracic exopodites are rapidly whirled round so that their tips describe a series of ellipses. The direction of rotation, and the probable positions taken up by the long-feathered setæ at different phases of the beat, are indicated in text-fig. 6*a*. At rest, the distal part of the exopodite with its setæ forms a spoon, open above and curving upwards towards the tip. During the upward and backward phase of the beat the setæ will be forced to spread out, so increasing the surface of resistance offered by the limb. The reverse will hold during the downward path of the limb, the setæ lying close together at the sides and above the axis. Thus, quite apart from any muscular alterations that may occur controlling the speed of rotation at various phases of the beat, a stronger effect will be produced by the upward backward stroke of the limb than by the downward stroke, and it is this upward and backward beat which is responsible for creating the two strong backward currents of water and for propelling the animal forward. The greater strength and number of the setæ forming the anterior edge of the "spoon" will aid the efficiency of this motion.

Dorsally and ventrally the incoming currents divide and pass to the sides, so leaving a small region of still water close to the body in the mid-dorsal and mid-ventral lines (text-fig. 6*b*). This still water on the dorsal side lies chiefly over the posterior part of the thorax, and from this source water is drawn which supplies the respiratory stream. Gills are not present, but the carapace is richly supplied with an ample circulation of blood. A pair of large veins enters the carapace fold anteriorly, and proceed along the lower margins. They supply the blood lacunæ which occupy the whole space inside the fold, and from which the blood is again collected and discharged into the pericardium opposite the heart ostia at the level of the third and fourth thoracic segments. Blood is also returned to the pericardium by lateral sinuses in the second to eighth thoracic segments lying immediately below the skin.

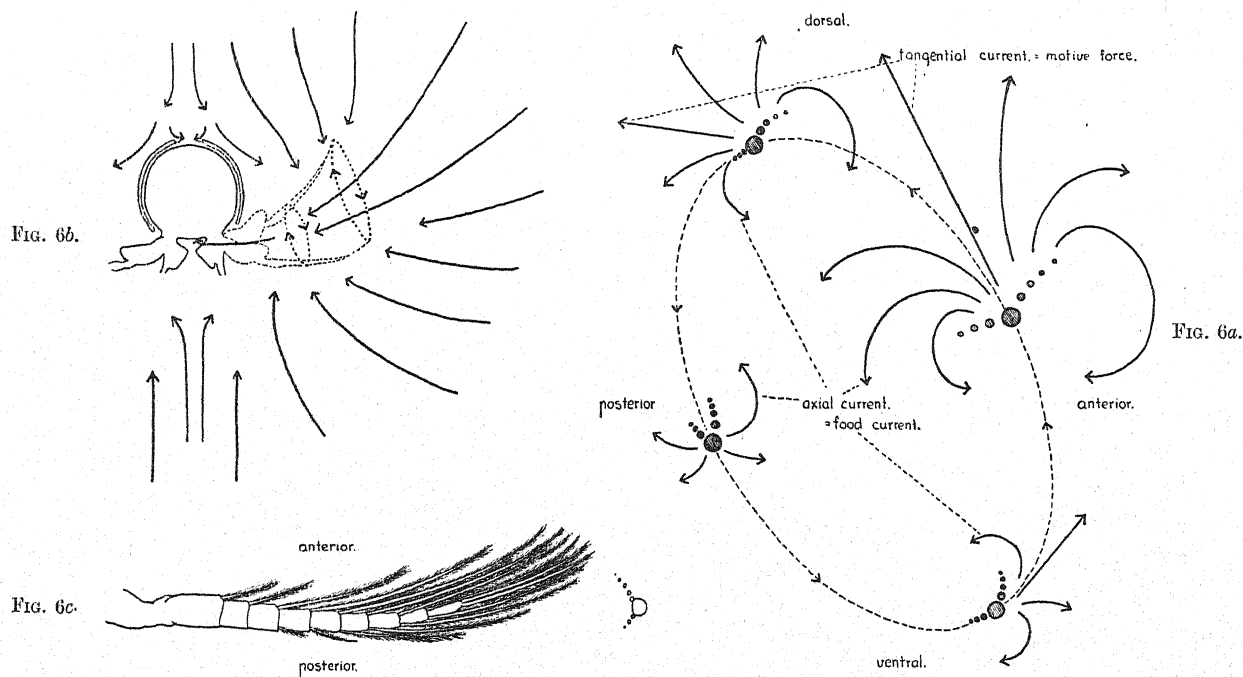
By the active movement of the first thoracic epipodite in the direction indicated in text-fig. 3*c*, water is bailed out of the space between the carapace and the body, and is replaced by water sucked in from the dorsal still area over the posterior thoracic region. By this means a rapid current is maintained under the carapace, gaseous exchange probably taking place chiefly through the inner wall of the latter and possibly also through the body wall over the lateral venous sinuses. The exhalent respiratory current passes out at the sides of the maxilla and maxillule. It then turns outwards or upwards and forwards over the mandible and mandibular groove and behind the eye. It is evidently caught by the lateral swirl and drawn upwards and backwards, so joining the main outgoing current. The movement of the



TEXT-FIG. 5.—Dorsal view of the animal swimming freely showing the currents produced in the surrounding water.  $\times 6$ .

upwardly projecting exite of the maxilla must, to a certain extent, assist in directing the course of the exhalent stream.

Besides the swimming currents, the rotation of each limb produces a food stream which is subsequently filtered. The currents produced by a single exopodite are indicated in text-figs. 6a and 6b. The rotating whip-like limb causes a conical swirl with the apex at the base of the limb, which draws water towards it from all directions. A strong stream is formed up the axis, flowing towards the base of the limb. The mathematical treatment of this current cannot be dealt with here, but it can be readily understood by a very simple experiment. If, in a large vessel containing water and at the bottom a layer of some precipitate, the water is stirred by a spoon, the precipitate will be sucked up the axis of the cone described by the



TEXT-FIG. 6.

FIG. 6a.—The diagram represents the tip of a single exopodite as it is whirled round, showing the positions of the setae with respect to the axis of the limb at various phases of the beat and the currents created in the water.

FIG. 6b.—The diagram indicates a thoracic transverse section of the animal, showing the rotation of one exopodite with the currents it produces in surrounding water.

FIG. 6c.—A dorsal view of a single exopodite, showing the arrangement of the lateral setae; and a diagrammatic section across this limb.

spoon. The spoon corresponds to the exopodite, its bowl corresponding to the feathered tip, while the more or less rigid hand holding the spoon corresponds to the attachment to the rigid base of the limb. The production of this axial stream can be understood from text-fig. 6a, which represents diagrammatically an end-on view of the tip of the exopodite as it completes one revolution. In any position the exopodite along its whole length tends to push water in front of it, but, in addition, as it moves through the water there will be a backwash of water round its sides to take the place of the water that has been pushed forwards. From text-fig. 6a it will be seen that whatever the position of the limb there is always a backwash towards the axis of its cone of rotation. It is this backwash that provides the water for the axial current. Further, at the tip of the exopodite, where the feathering makes it effectively broad and where the velocity is greatest, the backwash towards the axis will be much greater than at the base, where there is no feathering and the velocity is small. This will lead to a region



of high pressure at the centre of rotation of the tip and of low pressure at the base of the limb. Consequently, water will stream down the axis towards the body. It is the existence of these axial streams towards the base of each thoracic exopodite that causes the water to stream from all directions towards the sides of the body.

The axial streams along each exopodite pass between the limb bases and into the space enclosed by the inner flanges or the basipodites and the ventral body wall, and merge into one forwardly directed stream. This is joined posteriorly by two currents that pass forwards behind the eighth thoracic limbs. In fact, it is probably the main stream moving forward that sucks water in in this region. Anteriorly, the stream is narrowed down as it passes between the bases of the first thoracic limbs. When it reaches the level of the maxillæ it divides into two lateral streams, which pass out immediately behind the bases of the paragnaths through the overlapping combs of setæ and so join the exhalent respiratory currents that have already been described.

The motive forces causing the forward direction of this stream are probably three. Firstly, the actual pressure of the water in the axial currents forces the water in between the limb bases, and from the shape of these bases the water must be given a forward motion. Secondly, the exhalent respiratory current must suck water through the maxillæ. And thirdly, the motion of the whole maxilla and the vibration of its exite must suck water out of the food basin, and directly force it from the base of the limb in an outward direction.

Finally, one other water current remains to be mentioned. A groove extends along the sides of the body between the limb bases and the ventral edge of the carapace above (text-fig. 3a). In this channel the water flows backwards. This stream is doubtless induced by water from the apical parts of the exopodite swirls being trapped in the channel.

#### MOVEMENTS OF THE MOUTH-PARTS.

Before considering the various methods of feeding, an account of the movements of the mouth-parts must be given (fig. 5). The endopodites and basal endites of the first trunk limbs are rapidly rotated inwards, forwards, and slightly upwards, and then back to their initial position. This results in the long anteriorly directed upper setæ of the first endite being pushed backwards and forwards across the food basin and into the food groove between the paragnath bases. The remaining endites approach one another in the middle line, the dactylopodites actually meeting, and their stiff terminal setæ curving upwards towards the mouth.

The movement of the maxillæ is more lateral than that of the first trunk limbs (fig. 5). The basal endites, which, together with those of the first trunk limbs, form the lateral walls of the food basin, move backwards and forwards, the pair of long setæ borne by them actually reaching as far as the lower oral cavity. The remaining endites and the palps dip inwards and forwards into the deeper part of the food groove.

Each maxillule, as a whole, moves inwards in the transverse plane (fig. 5). At rest, however, the three pairs of long spines from the proximal endites already reach the corresponding setæ of the other side in the middle line. Inward movement thus results in a forward movement of the feathered tips of these spines in the groove between the paragnaths into the lower oral cavity. This forward movement may be aided by the presence of the pair of backwardly directed setæ from the lower edges of the proximal endites which lie outside the paragnath bases. Any inward movement of the endites would bring these setæ in contact with these bases, and this would tend to convert any directly inward motion partly into a forward one.

The mandibles, as well as the distal endites of the maxillules, move in the transverse plane. In both cases this leads to an approximation and separation of the biting edges. The mandibles at rest lie practically transversely; but during activity their outer ends are periodically rotated backwards. This gives a rolling movement to the bite, and is probably of the greatest importance for the grinding action of the molar processes as well as in assisting sheering by the incisor processes.

The range of movements carried out by the lips is less extensive than that of the appendages; but their movements, although slight, must be of importance in feeding. No direct observations of such movements could be made, but they can be inferred, to a certain extent, from the musculature.

The movements of the paragnaths are controlled by three sets of muscles. A median muscle, as already mentioned, extends from the deep groove between the paragnaths to the endoskeletal plate (fig. 2*a* and text-fig. 2*b*). Contraction of this muscle would result in a deepening of the food groove in this region and an approximation of the two paragnaths. The space between them would thus be narrowed and so would concentrate the food matter so that it might more easily be pushed forward by the maxillulary spines. Muscles producing the antagonistic effect are attached laterally to the paragnaths and inserted on the lateral body wall (text-fig. 2*b*). The third set of muscles is the most powerful, but is not directly attached to the paragnaths. In the ventral mandibular groove separating upper lip and paragnaths, two upwardly projecting skeletal tubes pass from points opposite the outer anterior corners of the paragnaths (text-fig. 2*a*). These tubes project into the body just behind the adductor muscles of the mandibles. Their inner ends are connected to the dorsal body wall by a group of large muscles inserted just behind and above the levator muscles of the mandibles. Contraction of these muscles would cause the ventral mandibular groove to be raised, and so tend to tip the paragnaths forwards more closely on to the mandibles. Movements of the paragnaths are thus possible in a variety of directions, and these movements which must alter the size of the food groove between the paragnaths, or the positions of the setose paragnath edges which form one of the openings to the oral cavity, are probably of the greatest importance in the feeding mechanism.

The labrum, unlike the paragnaths, is probably only slightly movable as a whole, but localised changes in shape are of importance. The armed lower edge overhanging the incisor processes can be lifted up by a pair of longitudinal muscles which pass to the anterior labral ectoderm. Dorso-ventral muscles in the middle of the labrum will have the opposite effect on the posterior edge (fig. 2*a*). The median group of setæ on the posterior face of the labrum can be directly moved by the median antero-posterior muscle. Many of these setæ are directed upwards and forwards, and so, by contraction of the muscle, they will help to scrape food upwards into the oral cavity and on to the molar processes. Other paired muscles radiate in various directions from the face of the labrum forming the walls of the upper oral cavity. Contraction of these muscles will increase the size of the upper oral cavity, and so help to suck food into it.

#### FEEDING HABITS.

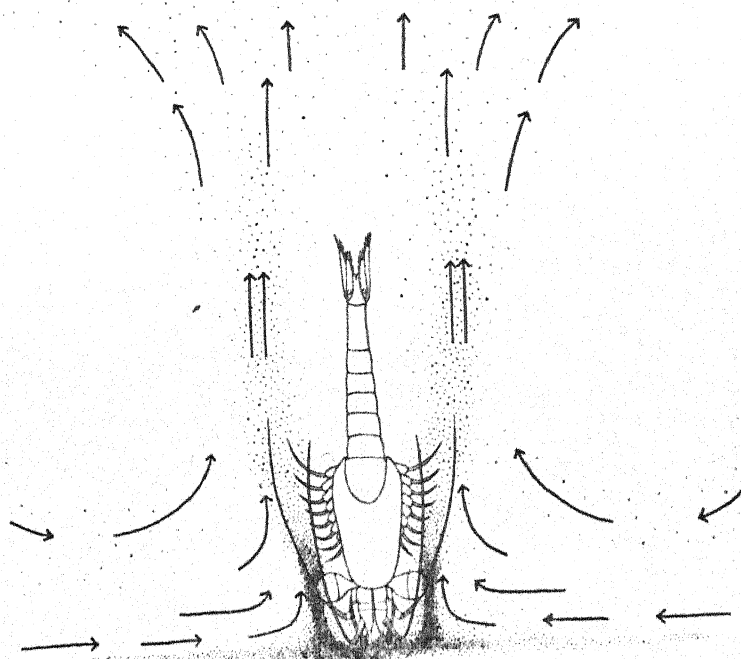
Hemimysis exhibits two distinct methods of feeding. It may feed either on suspended food material which it filters from the incoming food currents or on large masses of food which it picks up with its thoracic endopodites. In its established condition in the large tanks at Plymouth it is undoubtedly largely subsistent upon suspended food. The vast majority of individuals are always found swimming horizontally in swarms a few inches off the bottom.

They have never been observed to rest on solid objects by holding on with their thoracic endopodites in a lobster-like manner, as does *Macromysis*. Only occasionally are they seen making excursions into the mud or on to the substratum. However, when kept for observation in bowls of still water they show a much greater tendency to search the bottom, and will also feed very readily on large pieces of food.

In the tanks in which they occur, the fish, especially the flat fish, constantly churn up the bottom detritus, so that for some distance off the bottom there must be a plentiful supply of suspended matter. Further, owing to the different rates of settlement of the disturbed particles, the smaller particles must, roughly speaking, occupy the higher levels, the larger ones occupying the zone close against the bottom. It is probable that this gradient in the size of the suspended particles is an important factor in determining the level at which the *Hemimysis* swarm. Also, there must be for each size of individual an optimum size of suspended particles for filter feeding, and hence this gradient may also account for the fact that individuals of the same size usually swarm together. Certainly the larger individuals are found much closer to the bottom than are the smaller. The animals strongly dislike muddy water, probably because the food groove becomes choked and the filtering mechanism unworkable.

If the animals are kept in still sea water which contains little live plankton, then the suspended matter soon settles to the bottom, and the food becomes

insufficient for feeding by filtering during horizontal swimming. Under such circumstances the animals swim down to the bottom and take up a vertical position, resting on the antennal scales and inner flagella of the antennules as if on a three-legged support (text-fig. 7). The thoracic exopodites create the usual currents, which, however, are slightly modified owing to the presence of the substratum. The outgoing streams remain unaltered, but the streams towards the body from in front now flow parallel and close to the substratum approaching from all directions. On reaching the antennal scales they are drawn sharply upwards at the sides of the eyes and then follow the usual course. The general widespread drift over the substratum towards the body is thus converted into two localised, and therefore powerful, upward currents, and these carry with them a large mass of particles from the bottom. These pass directly to the outgoing currents, and are shot upwards into the water. They then disperse in all directions, and some are ultimately drawn in towards the body by the ingoing currents and so enter the food stream. That this is a very efficient



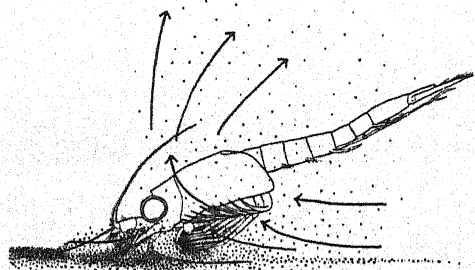
TEXT-FIG. 7.—View of animal resting head downwards on the substratum, showing the course of the currents created in the water and the manner in which particles are drawn up off the bottom by these currents and distributed in the water round the animal.  $\times 6$ .



mechanism for renewing the supply of suspended matter in the water can be seen experimentally. An individual with an empty stomach is placed in a small tank of sea water, on the bottom of which a layer of starch grains, stained with iodine, has been allowed to settle. The mysid usually assumes almost at once a vertical position resting on the bottom, and two dense streams of the coloured starch grains are seen to be drawn up at the sides of the head. These grains are carried upwards for a distance of 2 inches or more before they disperse. Very soon the lower layers of water become charged with starch grains forming a conspicuous cloud in the water round the animal, and these grains become drawn in with the food stream and pass into the stomach, the colour of which darkens in a few moments owing to the contained coloured starch. This is one method by which food is obtained off the substratum, but the food is here only utilised indirectly after it has passed into the water circulation induced by the thoracic exopodites. However, food lying on the bottom may be directly collected and eaten when suspended food is scarce. In a tank prepared as above, an individual may sometimes be seen to swim along the bottom with its body tilted at an angle of about 20 to 30 degrees (text-fig. 8). The inner flagella of the antennules and the antennal scales plough into the layer of starch, which is further disturbed by the antennal flagellæ being dragged along by the side of the body. As the animal moves forward the starch shovelled up in this way is seized by the thoracic endopodites, and the mass so collected held against the mouth-parts which convey the food to the mouth. Hemimysis will also plough up mud in a similar way, but it does so less frequently and does not devour the mud so readily as it does the starch.

#### FILTER-FEEDING.

The production of the food currents by the rotation of the exopodites of the thoracic limbs and their passage in between the bases of these limbs into the food groove has been described above (p. 228). An efficient arrangement exists which prevents these entrances into the food groove from becoming obstructed, in the form of the setæ already described on the thoracic limb bases which project across the lateral openings (p. 225). Any material collecting on these setæ tends to become dislodged and swept away by the backwardly flowing current between the limb bases and the edge of the carapace (see above, p. 229, and text-figs. 3a and 3b). In the male the lateral setæ on the penes similarly guard the posterior openings to the food groove. The penes are freely movable, and thus can rid themselves from any accumulated matter.



TEXT-FIG. 8.—Lateral view of an animal swimming along the bottom and ploughing up food particles with the inner flagella of the antennules and the antennal scales. A mass of food is collected and held by the basket of third to eighth endopodites and the mandibular palps. The arrows indicate the currents, the lateral exopodite swirl being omitted (see text-fig. 4).  $\times 6$ .

During filter-feeding the feeding reaction is different when the suspended food particles are few from when they are numerous. Isolated particles carried in by the food stream pass rapidly forward along the thorax and enter the narrow tubular channel between the basal endites of the first trunk limbs. This tube has as its roof the median ventral body wall, its walls are the bases of the first trunk limbs and more anteriorly the paragnath bases, while its floor is formed by the lower setæ of the basal joints of the first trunk limbs which overlap in the middle line. On reaching the widened food basin,

as already mentioned (p. 229), the food stream divides into two, and passes out laterally through the combs of setae from the basal endites of the first trunk limbs and maxillae. Food particles are thus deposited on these combs, or directly on to the long anteriorly directed spines from the basal endite of the maxillule and maxilla which project forward as far as the oral cavity. In any case it is undoubtedly the latter, together with the reduced anteriorly directed food stream, which pushes the food forwards into the mouth in the neighbourhood of the mandibular spine-rows (figs. 2 and 5). It is the basal endite of the maxilla, however, which is the only true filter in the mechanism. Its comb of setae is very closely and finely feathered, and effectively removes all particles from the outgoing food current. The combs of setae on the proximal endites of the first trunk limbs are only coarsely feathered and do not form a filtering plate.

The way in which particles from the food stream are retained can be clearly seen from sections of an animal which has been kept in a suspension of iron saccharate. The particles of iron saccharate are collected in a normal manner, and the animals live for an indefinite period in such a suspension. The particles remain sticking to the food groove and mouth-parts after sectioning, and by treatment with ferrocyanide become clearly recognisable by their blue colour. The diagrams in text-fig. 9 are made from such a series of sections. Particles are found throughout the food groove, but they are more concentrated deep down between the paragnaths near the mouth (text-fig. 9a). An even accumulation of particles is found on the ventral side of the combs from the proximal endites of the maxillae, but on no other appendage, and no particles are present in the path of the outgoing food stream (text-figs. 9b and 9c). Clearly, these combs must be filtering the food stream, the conclusion reached by direct observation. Collections of particles are seen on the setae of other appendages, notably the proximal endites and dactylopodites of the first trunk limbs and the distal endites and palps of the maxillae. These are particles already retained in the food groove, and are being pushed towards the mouth.

Food particles are probably retained from the food stream by two methods. Their passage may be simply checked, and, lying freely in the food groove, they may be carried forward by the anteriorly directed spines of the mouth-parts and the forward current. Or they may be retained directly on the maxillary filtering comb, especially if they are sticky, and can then only reach the mouth by being scraped off this comb by the proximal endite of the first thoracic limb. The arrangement of the maxilla and first thoracic limb is such that, if either of them moves, the maxillary comb is scraped against the first thoracic endite. It is also probable that isolated particles are partially sucked forwards from the filtering endites into the oral cavity by the contractions of its anterior wall, and in this way particles may pass directly on to the molar processes of the mandibles.

The above account describes the mechanism by which food is transferred into the mouth when the food particles are sufficiently scarce to be dealt with by the mouth-parts as they arrive from the food groove, so that no accumulation occurs in the food basin. When, however, the water contains a considerable amount of suspended particles, the feeding reaction is different. The movements of the limbs become more extensive, and, if the particles prove palatable, greater efforts are made to draw them into the ventral thoracic space. The inwardly projecting flanges of the basipodites are divaricated so that the size of the channel is increased, and in the male the penes stand slightly backward instead of a little forward, so that their lateral setae project far away from the eighth basipodites, thus leaving the posterior channels to the food groove widely open. Larger food particles collect to a considerable extent in the wide food groove behind the first trunk limbs. The basipodites of the trunk limbs vibrate

slightly, and the inwardly and forwardly directed setæ from their inner flanges assist in moving the food masses forward. All the mouth-parts become more active, and their distal extremities become functional. All the endites of the first thoracic limbs and maxillæ pack the food inwards and forwards and towards the biting endites of the maxillules and incisor processes. The maxillary palps form a floor below the latter, and prevent food falling away

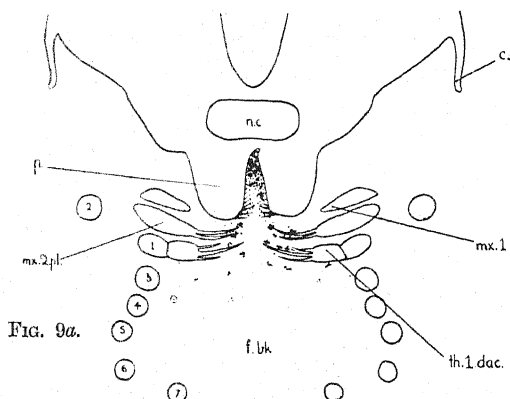


FIG. 9a.

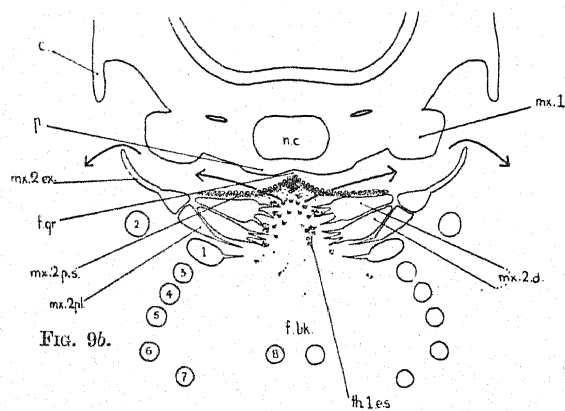


FIG. 9b.

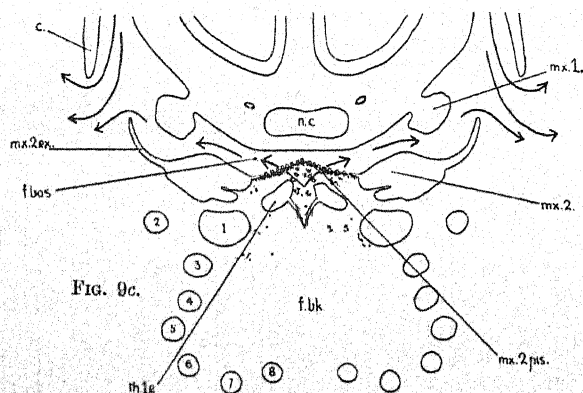


FIG. 9c.

TEXT-FIG. 9.—A series of diagrams of transverse sections at the levels marked in figs. 2b and 5, to show the filtration of particles from the food stream by the maxillary combs and the subsequent path taken by these particles. The diagrams were made from sections of an animal fed on iron saccharate.

FIG. 9a.—Section showing the food concentrated in the upper part of the food groove between the paragnaths. Into the lower part of the groove project the first thoracic dactylopodites and the maxillary palps.

FIG. 9b.—Section through the posterior part of the maxillary segment and cutting through the distal parts of the maxilla. The food stream from the food basin passes sideways through the comb on the basal endite of the maxilla, on which is deposited all suspended matter, and out between the base of the maxillule and the maxillary exite. Into the food basin project the distal maxillary endites, and the long setæ from the basal endites of the first thoracic limbs.

FIG. 9c.—Section slightly posterior to that of fig. 9b. The filtered food stream is seen joining the exhalent respiratory current, and the basal endites of the first thoracic limbs are cut in section. Text-fig. 2c is just posterior to text-fig. 9c, and shows the union of these endites with the first endopodite.

c., carapace; f. bas., food basin; f. bk., food basket formed by the third to eighth endopodites; f. gr., food groove; mx. 1, maxillule; mx. 2, maxilla; mx. 2 d., divided distal endite of the maxilla; mx. 2 ex., maxillary exite; mx. 2 pl., maxillary palp; mx. 2 p. s., filtering comb of setæ from the proximal maxillary endite; n. c., nerve cord; p., paragnath; th. 1 dac., first thoracic dactylopodite; th. 1 es., anteriorly directed setæ from the proximal endite of the first thoracic limb; 1, 2, 3, etc., first, second, third, etc., thoracic endopodites.

ventrally. The distal parts of the first and second thoracic endopodites are more flexible; they help to push food upwards toward the oral cavity besides forming a tray to catch particles which would otherwise be lost. They are also bent back and the tips used to scrape food forward from between the first thoracic limbs on to the biting mandibles and maxillules. The first pair of endopodites are used most frequently in this manner. A congestion of food sometimes occurs in the narrow passage between the bases of the first trunk limbs, resulting in a solid food mass in the wider food groove behind. A part of this mass is frequently bitten



off by the bases of the first trunk limbs and passed forward to the mouth-parts. The mandibular palps are also functional during such feeding. They are periodically rotated downwards, either together or separately, so that they hang vertically below the mandible. The broad bases of the palps present a large surface of resistance to the water, and possibly tend to check any forward flow over the mouth-parts. This would bring many stray particles of food to a standstill which would otherwise be carried away. They would then be more easily caught by the ends of the endopodites of the first and second thoracic limbs, which are continually clutching at the water in this region. Rarely the tips of the palps are bent right back and used to scrape the food forward from the base of the first trunk limbs.

The food which is thus accumulated in the neighbourhood of the mouth is bitten into by the distal endites of the maxillules and by the incisor processes of the mandibles. That bitten off by the former is pushed forward by the long maxillary spines on to the spine-rows of the mandibles (fig. 3a). That by the latter is pushed on to the left *lacinia mobilis*. Further biting of the mandibles must push this food mass upwards on to the right *lacinia mobilis*. From here it would pass to the left spine-row and then across to the right, and the latter would push it directly upwards on to the molar processes, where it would be ground and sucked up into the oesophagus by peristaltic action. It is highly improbable that any food mass would take this exact path, but the asymmetrical arrangement of the mandibles and the interlocking of the incisor processes, the *laciniae mobiles*, and the spine-rows provide a mechanism by which the simple lateral movements of the mandibles must transfer food from the ventral incisor processes to the dorsal molar processes. In this transference the adorally projecting hairs on the mobile paragnaths and on the movable floor of the upper oral cavity are undoubtedly of great functional assistance.

If the collected particles are unpalatable, those that have reached the mouth-parts are thrown out sideways, and no effort is made to collect smaller fragments that may stick to the combs of setæ on the maxillæ and first thoracic limbs. The first pair of endopodites are used most actively to scrape out the food groove and to remove foreign bodies. The chief reaction, however, to suspended matter not suitable for food and present in any quantity is a violent effort by the animal to swim out of such a region and to shake the body free from particles. This is doubtless necessitated by the automatic manner in which the food is collected regardless of its suitability.

The extensive labrum is not provided with large labral glands, as in the Branchiopoda, and little, if any, viscid secretion is present in the food groove and round the mouth. The collection of suspended particles appears to be carried out unaided by any food-entangling secretion.

#### FEEDING ON LARGE FOOD MASSES.

Besides being a filter feeder, *Hemimysis* also feeds from large solid masses of food which may be either living or dead. The nature of such food has been discussed at length by DEPDOLLA (1923). Large food masses are seldom secured by a horizontally swimming *Hemimysis* unless they are alive. Pieces of decomposing matter are frequently obtained from the bottom of the tanks. Where such detritus is lying thickest an individual may often be seen rapidly to dive into it and emerge carrying a corpse of another mysid or some other piece of organic matter. The food is held by the thoracic endopodites and consumed as the animal swims away. Such food masses vary greatly in size, from a *Sagitta* exceeding the mysid in length to particles which are simply too large to be dealt with by the filter-feeding mechanism. The food mass is held below the mouth-parts by the long third to eighth endopodites. The multi-

articulate propodites of these limbs renders their distal extremities very flexible, so that they can readily manipulate the food, turning it about in any direction. When the food mass has been caught and held by these endopodites it is suitably orientated and brought close up to the mouth-parts. This result is largely effected by the mandibular palps and the first and second endopodites. The palps either grip the food between them or bend backwards and press it over the mandibles. Their outward and downwardly projecting setæ from the distal joint are very effective in gripping the prey even if it has a smooth chitinous exterior (fig. 5 and text-fig. 3a). The endopodites of the first and second limbs hold the food close to the body like two pairs of clasping arms; the incisor processes and the distal endites of the maxillules directly bite into the mass, and the subsequent path of the food is as described above (p. 233). After every few seconds the whole mass is shifted about by the holding appendages, so that new surfaces are continually being held to the mouth. In this way such an unwieldy object as a *Sagitta* can be eaten by a *Hemimysis*.

It is clear that the two methods of feeding—the feeding on large food and the filter-feeding—are quite independent, and, although we have not observed both methods of feeding being carried on at once, it is highly probable that this does take place.

#### DISCUSSION.

The mysid *Praunus flexuosus*, Müll., studied by DEPDOLLA (1923), is more than twice the size of *Hemimysis lamornæ*. It does not appear to differ from it in any important point in the structure and arrangement of its limbs. Its method of swimming also appears to be similar. It is thus highly probable that the feeding habits and the use of the appendages in the two forms will be in all essentials the same. However, DEPDOLLA's account differs very considerably from the account we have given in this paper.

He rightly observed the two methods of feeding—firstly, by catching large food masses; and, secondly, by the collection of suspended particles. His account of the water currents produced around the animal is very scanty and differs essentially from our observations. Firstly, he states that two symmetrical water streams inclined at an angle of 30° to the axis of the body approach the antennal scales from in front. Water certainly does stream roughly towards the antennal scales from in front, but this is only part of the general drift towards the body. It becomes localised more markedly into two streams when the animal is standing on its head to feed (p. 231), but in this case the streams are parallel to the body. However, he states that the two streams unite into a single stream that flows backwards between the thoracic endopodites, and brings all floating particles into the neighbourhood of the mouth. Here they are caught by the first and second trunk limbs and by the maxillæ. We are quite certain that this account is totally wrong. Firstly, there is no water-stream flowing backwards between the trunk limbs. Most of the water approaching the animal from in front on reaching the level of the antennal scale is drawn upwards to the dorsal level of the body, where it passes directly backwards into the strong outgoing posterior currents (p. 226). The remainder is drawn into the lateral swirl produced by the thoracic exopodites. None at all passes ventrally between the trunk limbs. Secondly, while DEPDOLLA describes the method by which the mysid feeds on larger food as essentially the same as that which we have described for *Hemimysis*, it is difficult to see how he would reconcile his account with the existence of his backwardly directed food stream. Such a stream would inevitably tend to wash away any large particle held by the endopodites, and a food particle such as a lump of bottom detritus would certainly be broken up and washed backwards away from the mouth. Thirdly, the arrange-

ment and movements of the mouth-parts, especially the mandibular palps with their very broad bases (figs. 1 and 5), make it highly improbable that any effective food stream would enter the mouth region from in front.

The primary fault in DEPDOLLA's observations was his inability correctly to observe the water currents around the animal. But, in addition, he made no attempts to analyse the main stream into the constituent swirls caused by the separate thoracic exopodites, neither did he make any detailed observations on the general structure of the animal and the interrelationships of its appendages. From these deficiencies in the observational work, together with the reasons we have given above, we consider that DEPDOLLA's account is essentially incorrect.

Detailed observations on the feeding habits among the Malacostraca have so far been limited, with the exception of DEPDOLLA's paper, to the Decapoda, and among them only *Palamon* and *Carcinus* have been studied at all fully (BORRADAILE, 1917, 1922). In these forms, however, there is no filtering mechanism, and it is in the possession of such a mechanism that the chief interest in the feeding of *Hemimysis* lies. This interest has been greatly increased by the recent interesting work of STORCH (1914-25) on the feeding habits of certain Branchiopoda and Copepoda. In all these "filter-feeding" forms STORCH describes a mechanism that can be divided into four parts: (1) a pump or some other mechanism for attracting the water carrying the suspended food particles to the mouth-parts; (2) an apparatus for abstracting the food particles from this water, termed by STORCH the filter apparatus; (3) an exit for the filtered water; and (4) an apparatus for carrying the collected food forwards to the biting mouth-parts. In *Hemimysis*, considering only the limbs in front of the second thoracic limb, all the constituents are present. The suction-pump is provided by the maxilla. The filtering apparatus consists of the first endite of the maxilla. The exit tube for the filtered water is mainly between the maxillary exite, the maxillule, and the body wall. The apparatus for carrying the filtered food from the filter on to the biting mouth-parts consists of the proximal endite of the maxillule, together with the long-feathered seta on the proximal endite of the maxilla, and the basal endite of the first trunk limb.

The existence of the four constituents of the filter-feeding mechanism is not in itself of much significance, because together they merely constitute what we know as a filter mechanism, and the absence of any one of them would render the whole apparatus unworkable. But *Hemimysis* is peculiar in that the mechanism for bringing the food bearing water to the mouth consists of two distinct parts, the maxillary suction-pump and the thoracic exopodites. The latter suck the water into the exopodite swirls and force it anteriorly along the ventral food groove, while the maxilla sucks it out of the anterior end of the food groove and forces it into the exhalent stream. It is thus obvious that while the two parts work together the maxillary part is independent of the other, and would still function in the absence of the thoracic exopodites. This independence allows the possibility that the part played by the thoracic exopodites may have been secondarily added to the more anterior filtering mechanism, the evolution of the "swirl" mechanism of food gathering having evolved from an essentially swimming reaction long after the establishment of the anterior maxillary apparatus.

A feeding mechanism which shows an interesting resemblance to that of *Hemimysis* is that of *Apus*. In this form, according to LUNDBLAD (1920, p. 93), the limbs immediately behind the mouth are used for seizing and feeding upon large food particles, while those behind are used simply for respiration. Now, STORCH points out (1925-26, p. 84) that these posterior limbs must automatically collect minute suspended food. While we cannot agree with the reasoning by which STORCH deduces this fact we have our own reasons for believing it to be so



(p. 244), so that we have in *Apus*, as in *Hemimysis*, a feeding mechanism, voluntary for large food in front, automatic for minute food behind.

A comparison of the feeding mechanism of *Hemimysis* with that of *Diaptomus*, as described by STORCH (1925c), also reveals interesting similarities. In both forms the maxilla acts as a true filtering mechanism; and in *Diaptomus* this is, according to STORCH, the sole method of food gathering; but, whereas in *Hemimysis* the maxilla by its own activity sucks water through its fringed endites, in *Diaptomus* the maxilla is a passive filter. It remains stationary and the water is sucked through it. The cause of this suction is a current drawn from the main locomotory backflow of water, and caused to pass close against the body on the outer side of the maxilla by a very rapid backwards and forwards movement of the maxillary exite. The food material retained by the maxilla is combed forwards on to the mandibles by the endites of the maxillules. In *Hemimysis*, also, food material is pushed forwards by the maxillary endites, but the latter do not act as combs scraping the food off the maxillæ. This is carried out by the setæ of the basal endite of the first trunk limb.

The main difference between these two forms is thus the different methods by which the food stream is caused to pass through the filtering apparatus. However, from STORCH's account and from his figures it is clear to us that a factor of equal importance to the sucking action of the maxillary exite is the backwash in the neighbourhood of the mouth resulting from the swimming activities of the second antennæ and the palps of the mandibles and maxillules. As we explain later (p. 244), between such backwardly beating structures as these swimming appendages there must exist a backwash, and this, together with the large upper lip projecting downwards in front of the mouth, must result in water being sucked in between the maxillary endites. The action of a large labrum in sucking water into the mouth region was explained in connection with the feeding of the nauplius of *Estheria* by CANNON (1924) (see also later, p. 248). We thus consider that in *Diaptomus*, also, the food stream is brought to the mouth partly by limbs other than the mouth-parts; but, whereas in *Diaptomus* these accessory limbs are the preoral and oral limbs, in *Hemimysis* they are the trunk limbs.

In *Daphnia*, STORCH (1924) has also described in great detail the "filter-feeding" mechanism, and here, again, he describes the four separate constituent parts. However, we consider that STORCH's account is not completely correct, and that the method of feeding as we describe it differs from that of *Hemimysis* in certain very vital points. He states that the structures which suck in the food-bearing current are the endites of the third and fourth trunk limbs. These endites are placed almost vertically with their setæ pointing upwards into the groove. They diverge slightly from behind forwards, and in passing upwards towards the trunk they slope inwards (CANNON, 1922, p. 221) (this agrees with STORCH's figures). From the fact that they are nearest together at their posterior ends the outwards movement sucks in the water from before backwards. STORCH states that in the inwards movement the ventral edges come together first and then the more dorsal fringed portions. This results in the water being forced upwards into the food groove. Now, STORCH maintains that this filters off the food particles, and presumably the latter are deposited on the combs of the sucking endites. In any case, he states that these filtered particles are carried forwards to the mouth by the action of the gnathobases of the second trunk limbs. It is on these last two points that we cannot agree with him.

Firstly, if the endites of the third and fourth limbs are actually filters in the sense that the word "filter" is ordinarily used and in the sense that the maxillæ of *Hemimysis* and of *Diaptomus* are filters, then the food particles must be deposited on them. But this is not the case. If a *Daphnid* is fed with iron saccharate and subsequently treated by the ferrocyanide

method, there is no layer of particles to be seen on the inner face of these endites such as would occur on the ventral face of the maxilla of Hemimysis, and this we take as clear evidence that these endites are not actually filtering off the food particles. We agree that they do prevent particles from escaping from the central filter chamber, but this is quite different from filtering those particles. An example may make this distinction more clear. Mud or detritus in a stream can be prevented from passing down stream by sweeping a brush backwards and forwards up against the stream. In this case the mud is mainly held back by the force of the water currents being swept against it. Some particles will stick to the brush, but the majority will be pushed back away from it. Now, this is quite different from blocking the stream with the brush and letting the force of the stream carry the mud particles against it, where they will be filtered off. We emphasise this difference, because we see no reason for assuming that the real filtering action of the maxillæ of Diaptomus and Hemimysis has been evolved from the sweeping action, or paddle action as we call it, of the Daphnid trunk limb.

The second point on which we disagree with STORCH is in the function of the gnathobases of the second trunk limb.

STORCH maintains that these sweep the food particles off the filtering combs of the third and fourth trunk limbs into the food groove. He gives a somewhat diagrammatic figure showing the setules on the setæ of the gnathobase pointing towards the endites that they are supposed to comb. We have not been able to see anything so definite as his figure. From our sections the setules simply point irregularly towards the food groove. STORCH also considers that the gnathobase pushes the collected food forwards along the food groove on to the maxillæ. But of the ten setæ on this gnathobase only three point definitely towards the mouth, the remainder pointing posteriorly; and, since the movement is mainly dorso-ventral, it is difficult to see how it can sweep particles anteriorly.

We believe that the account given by CANNON (1922) for *Simocephalus* is essentially correct. The food bearing water is sucked in by the outward movement of the endites of the third and fourth trunk limbs, and, "since they are not placed vertically, but are slightly further apart at their proximal ends than at the end of the comb of setæ in the food groove, the outward movement, in all probability, causes a small backwash in a forward direction in the food groove." While this statement is correct it is not complete. The fact that the endites slope inwards as they pass upwards would, on the outward movement of the endites, simply cause the water to pass upwards into the food groove. This upward movement is, however, more probably mainly due to the fact, as stated by STORCH, that in the inward movement of the endites their ventral edges come together before their more dorsal portions. However, we consider that it is also on the inward movement of the limbs that the water sucked into the "filter chamber" between the endites is caused not only to pass upwards, but is forced forwards along the food groove. Just as the water is sucked in between the endites from before backwards on their outward beat, so it is forced forwards on their inward beat, and this is simply a result of the fact that they are further apart in front than they are posteriorly.

The gnathobases of the second trunk limbs can be divided into two portions. The posterior part sweeps the filter chamber free of particles into the food groove, so that the actual food collecting from the food stream is carried out by this gnathobase and not by the filtering action of the third and fourth trunk limb endites. As we have already stated, STORCH also considers that the gnathobase assists in collecting food into the food groove, but he considers that it is primarily filtered off by the third and fourth endites.

If a Daphnid is treated by the iron saccharate method, the sections show the particles of iron being gathered on the hairs of the gnathobase of the second trunk limb; but there



is no layer of the particles on the inner side of the third and fourth trunk limb endites. The whole of the filter chamber shows scattered blue particles, and these are concentrated only on the tips of the gnathobase pointing towards the food groove.

The food particles so gathered we consider are then carried forwards by the current towards the mouth, and in the neighbourhood of the maxillules the anterior parts of the gnathobases sweep the secretion of the labral glands on to them, so collecting them into a coherent mass which can then be pushed forwards by the maxillules on to the mandibles, the water currents at the same time passing outwards at the bases of the first trunk limbs. On the question of the function of the labral glands in the feeding mechanism, STORCH will not commit himself. He states (1924, p. 211): "Wieweit beim Zusammenbacken der Nahrungsteilchen im Bereich des Vorbringesapparates das Sekret der Oberlippendrüse eine Rolle spielt, darüber stehen mir keine eigenen Erfahrungen zu Gebote." However, in such a form as *Daphnia*, it seems highly improbable that the food gathered in the food groove would remain there and ultimately be passed to the mouth unless it was held together by some secretion. At the anterior end of the food groove in front of the endites of the third and fourth trunk limbs there must be considerable currents passing out laterally, and small isolated particles would necessarily be washed away before they reached the mouth. In considering this question it is misleading to consider the feeding of *Daphnia* on such things as suspended carmine particles. These normally adhere, and are therefore not of much use in observing feeding mechanisms. It is isolated particles, such as single diatoms, that must be considered, as it is upon this sort of food that *Daphnia* feeds.

In support of the importance of the labral glands in the food-gathering process, CANNON mentioned their precocious development in the nauplius of *Estheria* (fig. 14). In this form a food current is sucked into the mouth region by the presence of a large labrum, and, obviously, the water cannot pass into the mouth. In addition, there is no apparatus for pushing the food into the mouth except the single masticatory setæ on the antennæ. It is very difficult to imagine these setæ pushing a single diatom into the mouth, but, on the other hand, a viscid mass of secretion in which the diatom was embedded could easily be pressed forwards into the mouth.

To summarise, while STORCH considers that the feeding process is, in a *Daphnid*, essentially a filtering process, we consider that the food is carried to the mouth by the water currents in which it becomes concentrated by the action of the gnathobase of the second trunk limb, and finally entangled in a viscid secretion in the neighbourhood of the maxillules. The latter pass the entangled mass on to the mandibles. Thus at no time is there a true filtering process such as occurs in *Hemimysis*, and, according to STORCH, in *Diaptomus*. Filtering does take place necessarily to a certain extent. It would be impossible to move the comb-like endites of the third and fourth trunk limbs through the water without some water passing through its setæ, and hence a certain amount of filtering would be carried out; but we consider that this is a secondary result, the main action of the endite being that of pushing the water in front of it, and for this purpose, as STORCH has shown, the arrangement of setules on its setæ admirably fits it. It may be mentioned here that NAUMANN (1921, pp. 9-11) also agrees in considering the anteriorly directed current in the ventral food groove as an important factor in the feeding process.

The various types of feeding in the Branchiopoda, and in fact in the Crustacea generally, STORCH derives from a homopodial type the most primitive modern representative of which he considers to be that of the Anostraca. He accepts LUNDBLAD's description of the feeding process, but with one reservation. LUNDBLAD states (1920, p. 86) that from a ventral posteriorly directed current produced through the locomotory activity of the trunk limbs a series of currents



pass upwards between the limbs to the ventral food groove. Here they unite into a more powerful anteriorly directed current along the food groove. Now, STORCH (1924, p. 220) does not consider this ventral food stream important in transporting the food collected from the currents towards the mouth. He considers rather that it is chiefly by the sweeping action of the gnathobases, or, in the case of *Chirocephalus*, of the proximal part of the first endite, that this is carried out. He states (1924, p. 221): "Es gibt kein als Wasserstrom zu bezeichnendes Bewegungs-phänomenen in der Bauchrinne, sondern nur ein Kehrvorrichtung, die ruckweise die abgelagerten Nahrungspartikelchen vorwärts befördert." But in *Chirocephalus* the walls of the food groove are formed by the spines of the proximal endites of the trunk limbs, and these all project either dorsally towards the food groove or posteriorly. The spines which project forwards are outside the others. The forwardly projecting spines on any one limb are covered over on the median side by the backwardly projecting spines of the limb in front, so that the supposed gnathobasic portion of the proximal endite, if it did function in pushing food forwards, would push it in between successive limbs and not in the food groove. STORCH also considers the trunk limbs of *Chirocephalus* as *eine Filtrationseinrichtung* (1925e, p. 361), and he constantly compares them with the "filtering" endites of the third and fourth trunk limbs of the Daphnids. However, he does not give any indication of how the residue filtered off by the trunk limbs is transferred into the food groove. As in the case of the Daphnids, we do not consider the limbs essentially as filters, and we agree with LUNDBLAD that an anteriorly directed stream in the ventral food groove is one of the main factors in the feeding mechanism.

Having come to the conclusion that the Anostracan method of feeding is the most primitive, STORCH now takes the Anostracan limb as the least specialised, and derives the other types of feeding limbs from it. Thus the limb of *Apus* is derived from that of *Chirocephalus* by the development of the gnathobase, and not *vice versa*. The proximal endite of the *Chirocephalus* limb is supposed to have become divided into two, the proximal portion becoming the gnathobase. There are two main reasons why we cannot accept STORCH's views. Firstly, in any continuous series of limbs which do not show any marked differentiation into tagmata (*i.e.* in which any structural gradations are continuous in the series) it is in the most posterior limbs that the more primitive characters are found,\* and this applies most to the limbs associated with feeding. Now, BORRADAILE (1926, pp. 197-98) has shown that the last trunk limb of *Chirocephalus* exhibits an extra endite occupying the position of a gnathobase, so that we think it probable that the anterior limbs have lost their gnathobases rather than that the posterior ones, where the gnathobase would be of least use, have developed them. The second reason for disagreeing with STORCH is not so much that we cannot regard the Anostracan limb as primitive, as that the recent work of SCOTFIELD (p. 13) on *Lepidocaris* clearly indicates that the *Apus*-like limb arose from a limb totally unlike that of *Chirocephalus*. In *Lepidocaris* the posterior trunk limbs are simple, biramous, foliaceous appendages (text-fig. 13), and we take the view that these represent the most primitive of the trunk limbs. In passing forwards, the endites, and the setæ on these endites, become more pronounced, and, in addition, a definite gnathobase is formed. At the same time, the exopodite shifts its position on the limb axis so as to arise near the base of the limb (text-fig. 13), and thus on the first trunk segment we have a limb which closely resembles the typical trunk limb of *Apus*. The gnathobase is remarkably similar. The exopodite represents the flabellum, and, in fact, it is only in the more distal portion of the limb that there is any marked difference. Here the distal endite is armed with very strong setæ which recall those on the trunk limbs of *Chydorus*. Probably in *Lepido-*

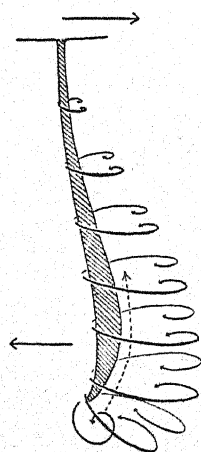
\* Since writing the above, Dr CALMAN has expressed the same opinion, *Nature*, vol. cxviii, 1926, p. 89.

caris this development was associated with a similar habit of crawling over the surface of plants as FRANKE (1925) has described for *Chydorus*.

We consider, then, that SCOURFIELD's accurate and brilliant description of *Lepidocaris* suggests very strongly that the primitive Crustacean limb was a simple, biramous, foliaceous appendage, and that from it the "phyllopodium" such as occurs in *Apus* was derived. The Anostracan limb may have arisen from a limb similar to that of *Apus* and the anterior trunk limbs of *Lepidocaris*; or, on the other hand, it may have developed independently from the biramous type. On this point we have no definite morphological evidence, but, as we explain later, from a consideration of the feeding habits we incline to the former view.

The two main faults in STORCH's reasoning appear to us to be that he considers the food-gathering limbs essentially as filters, and that the action of the anteriorly directed food current in the median ventral food groove is negligible. If, now, these limbs are regarded essentially as paddles, then they must gather food and direct it forwards by a current along the ventral food groove towards the mouth, whether or not they are provided with gnathobases. In order more fully to illustrate this idea, it is necessary first to consider the currents produced in a fluid by a simple paddle-like structure.

When any paddle-like structure moves through water there is always, as with the swirl production of the thoracic exopodites of *Hemimysis*, a backwash of water round the sides and over the tip. Further, this water in passing round the edges of the paddle is given a vortex motion. Text-fig. 10 represents the side view of a paddle moving from the right to the left. It can also represent the side view of any simple swimming limb, in which case the animal bearing it would be moved to the right. The arrows indicate the backwash, their length denoting its extent. At the tip, where the paddle is moving fastest, the backwash is naturally greatest. The water passing round the sides, it is clear, is given no impetus towards the base of the paddle, but the vortex of water passing over the tip has a definite upward motion. Now, the momentum of this vortex must carry water up the front surface (right-hand side in the figure) of the paddle, and the degree to which it will pass upwards is proportionate to the momentum of the vortex. This, in turn, is dependent upon the speed at which the tip of the paddle is moved through the water. This means that the faster the paddle is forced through the water the greater will be the flow of water up its front face. It follows that in any series of backwardly beating swimming limbs there will always be an upwash of water or eddy current close against their front surfaces. Actually there will also



TEXT-FIG. 10.—Diagram representing the backwash and eddy currents produced round the sides and tip of a paddle moving from right to left.

be a similar current up their posterior faces, but this will be much weaker than the anterior, owing to the forward stroke of the limb being weaker than the backward (the effective swimming stroke).

While the speed at which the limb is moved through the water partly determines the amount of the backwash, the breadth of the limb is obviously another determining factor. The broader the limb the greater the backwash, since a greater amount of water will be pushed backwards. Now, we consider that this backwash is an essential feature in the food-gathering mechanism of the phyllopodial limbs. It is thus interesting to note that other limbs which are entirely swimming appendages and do not collect any food such as the second antennæ of the *Daphnid*, have given up the broad phyllopodial structure and branched out into a structure just as effective as a paddle, but of no use as a food gatherer, since the backwash

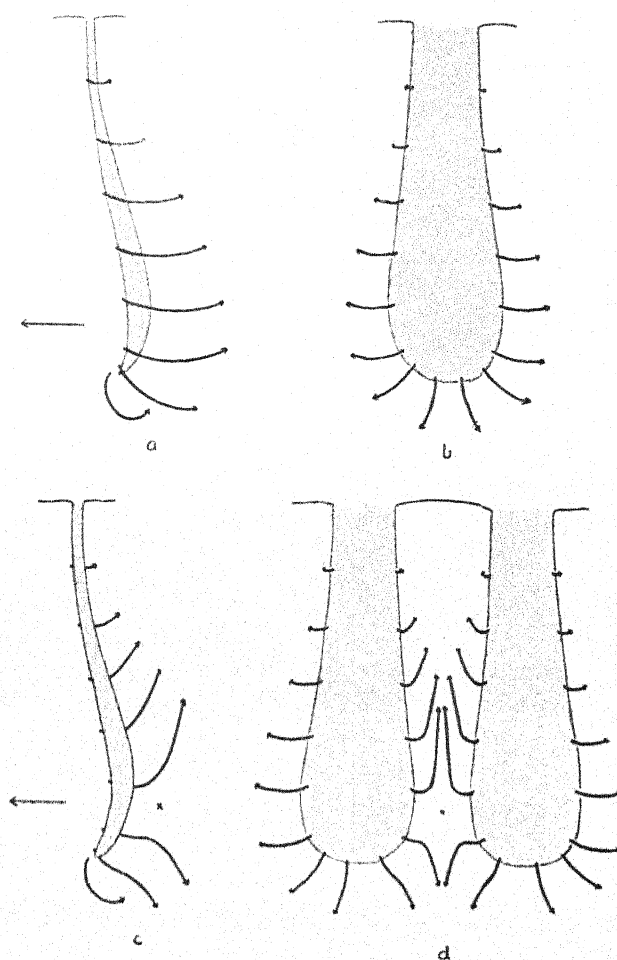
would extend simply along the front of the joints and setæ, and would not be directed in any special direction.

We wish to emphasise that the backwash produced by any paddle or flat limb is not merely a small current to be neglected, a current that may or may not occur, but that it is an absolutely necessary result of the movement of any such paddle through water. Water is simply a fluid exhibiting a certain degree of viscosity, and as such no paddle can possibly move through it without producing the backwash currents that we have described. In considering any swimming organism, the presence of the backward-flowing stream is taken for granted, but it is usually forgotten that for the production of that stream there must, of necessity, have been corresponding backwashes round to the front surfaces of the swimming limbs.

We will now consider the currents resulting from a pair of such paddles placed parallel to each other with a comparatively narrow space between them. Text-fig. 11*b* shows the backwash produced by a single paddle when viewed from in front, the length of the arrows, as before, indicating the extent of the backwash. The amount of water passing round the sides is clearly at a maximum near the tip. If a pair of such paddles are placed sufficiently near to each other, the backwash in between the paddles and near the tips becomes crowded, as there is insufficient room for the water to pass in between the paddles, and, consequently, in this region a state of high pressure is set up. At the bases of the paddles the backwash will be zero, and so there will be no extra pressure. Thus, near the tips the pressure will be high, while at the bases it will be normal. Now, the water must pass up from the region of high pressure to that of low; that is, the backwash between the paddles must be deflected upwards towards their bases (text-figs. 11*c* and 11*d*).

Instead of a pair of parallel paddles, consider now a paddle moving comparatively close to a flat surface. The same reasoning applies here as to the pair of paddles. The flat surface crowds the water near the tip of the paddle and so creates a region of high pressure, so that again the backwash is given an impetus towards the base of the paddle. Thus, text-fig. 11*c* will do for the side view of a pair of paddles or of a paddle moving close against a flat surface.

Before applying these ideal cases to the consideration of various Crustacean forms, there is another point to be considered arising from the fact that in *Lepidocaris*, *Trilobita*, etc., the

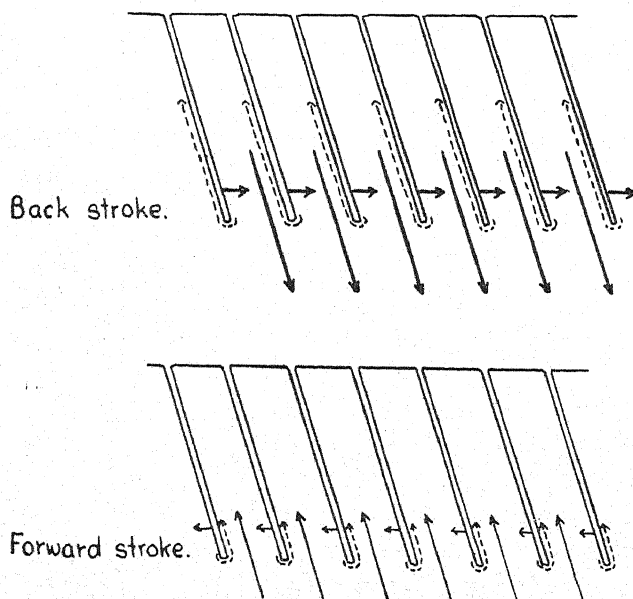


TEXT-FIG. 11.—Diagram representing the backwash round the sides of a single paddle (*a* and *b*) and of a pair of paddles (*c* and *d*). *a*, side view of a single paddle; *b*, front view of a single paddle; *c*, side view of a pair of paddles (only the backwash between the paddles is indicated); *d*, front view of a pair of paddles. The *x* indicates the region where the backwash becomes crowded.



limbs are arranged in a series, and in the position of rest they overlap each other. Now, on the forward movement of the limbs, to begin the back stroke the space between the limbs is enlarged and so water is sucked in to occupy this space. On the back stroke (the effective swimming stroke) the space between the limbs diminishes, and so the water is forced out again. Now the forward movement of the limbs is effectively slow, and consequently the momentum of the water rushing in is small. On the other hand, the back stroke is rapid and the water is forced out again with a comparatively big momentum (text-fig. 12); that is, the momentum of the water forced outwards is greater than that of the water sucked inwards, and consequently this action of the limbs in sucking water into the inter-limb spaces cannot represent the momentum which carries the water up to the bases of the limbs and so into the food groove.

Consider now a Crustacean with a double row of parallel-swimming appendages arranged



TEXT-FIG. 12.—Diagram representing how water may be sucked in and out of the spaces between any serially arranged series of flat appendages. The upper figure represents the powerful back stroke and the lower represents the weak forward stroke. The length and thickness of the arrows indicate the power of the current.

along the whole trunk and projecting downwards. The swimming stroke of these limbs will cause water to be thrown backwards. This will result in a backwash to the front of the appendages. Owing to the limbs being close together, this backwash in between the limbs will be given an upward motion. The backwash thus has an anterior and a dorsal momentum, and it will hence pass obliquely upwards and forwards between the limb bases, *i.e.* it will produce the anteriorly directed current along the mid-ventral line of the body. In addition to this forward current between the limb there will be up the front and back surface of the limbs, but more especially up the front, the eddy currents that we have shown must exist up the faces of any paddle.

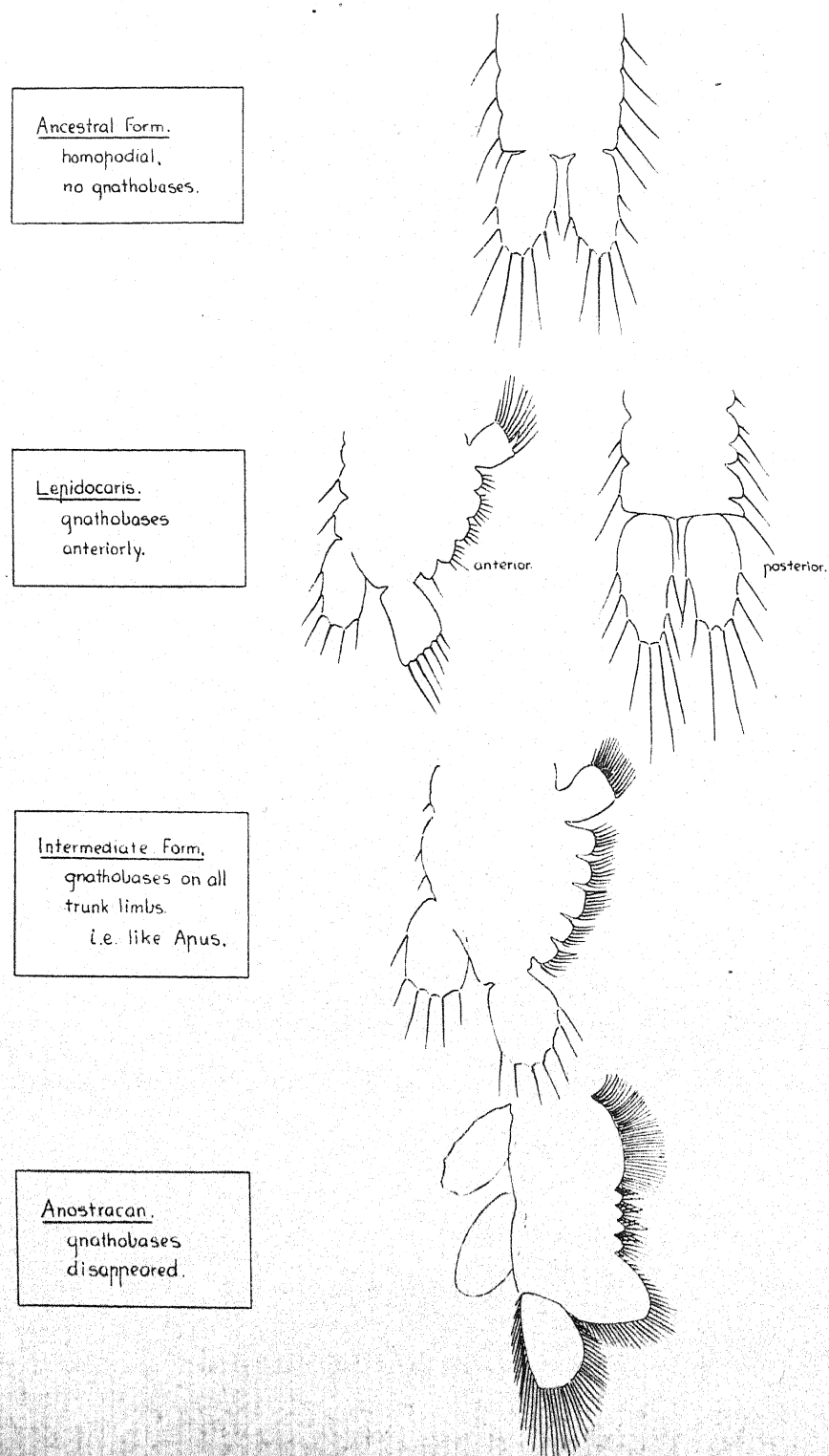
It is from such a form as this that we imagine the typical "Phyllopod" type of feeding to have evolved. In *Lepidocaris* we have a form closely resembling this primitive type. Here, however, the second antennae are large, well-developed, biramous, swimming organs closely resembling those of *Daphnids*. They are well developed in the early metanauplius, and, without doubt, represent a larval adaptation. In the adult we believe that while they persisted as swimming organs the trunk limbs were at least as important. A modern form closely resembling *Lepidocaris* in this respect is to be found in a larval stage of *Chirocephalus* before the second antennae have dwindled and given up their swimming function. In such a form the trunk limbs are responsible for the steady motion through the water, while the second antennae are used mainly to make sudden quick movements. The posterior trunk limbs of *Lepidocaris* are simple foliaceous appendages arranged in a parallel series. They are biramous; but, from the point of view of a feeding mechanism, this is probably of little importance. In fact, in passing anteriorly, the biramous nature of the appendages becomes of quite a secondary nature. Now, such a paired row of simple appendages must have caused a food current to

pass anteriorly towards the mouth, and we believe that it was by the production of such a food stream that *Lepidocaris* fed. Anteriorly the trunk limbs have developed gnathobases, and these undoubtedly arose as adaptations to assist the food in this food stream towards the mouth. The first post-oral limbs have become completely modified and are practically identical with maxillules of modern *Daphnids*. This fact, combined with the fact that *Lepidocaris* possessed a well-developed labrum and probably well-developed labral glands, suggests that in the method of feeding a viscid secretion of the labral glands was an important factor.

SCOURFIELD, in his monograph on *Lepidocaris*, considers, in view of the differences that exist between this form and the modern Anostraca, that it should be placed, side by side, with the other orders of the Branchiopoda rather than being considered as ancestral to the Anostraca. We hold rather that it does represent a form from which the modern Anostraca could have been derived. The fact that in *Lepidocaris* the clasping organs are situated behind the mandibles, while in the Anostraca they are developments of the second antennæ, we consider of little significance. In certain other groups, *e.g.* the Ostracoda, the clasping organs occur on various segments. The main differences appear to us to be, firstly, the presence of swimming antennæ in *Lepidocaris* and their absence in the Anostraca, and of the gnathobases on the anterior limbs of *Lepidocaris* and their absence on the limbs of the Anostraca, with the probable exception of the last trunk limb. These two differences are probably closely correlated. The disappearance in the Anostraca of the large swimming antennæ necessitated a compensatory enlargement of the trunk limbs. Thus *Lepidocaris*, in correlation with its method of feeding, leads on to a form with gnathobases and endites on all the trunk limbs. This hypothetical intermediate form gave up its swimming antennæ, and to compensate for this the trunk limbs enlarged to such an extent as to obliterate almost completely the endites and the gnathobases. These views are summarised in text-fig. 13.

We do not mean to imply that the modern Anostraca collect food by the simple process we have suggested for *Lepidocaris* and its forerunners. The feeding of *Chirocephalus* is undoubtedly much more complicated; but we maintain that this process is based essentially, not on a filtering action of the limbs, but on a paddle action, with the necessary anteriorly directed backwash along the food groove.

STORCH's work on the Branchiopoda led him to consider the possible methods of feeding of the Trilobita; and, in order to bring these into line with the modern Crustacea, he has had to suggest that the foliaceous part of the limb usually termed the exopodite is really the endopodite and *vice versa* (1925-26). As he justly admits, he has not been able to examine the actual American specimens upon which all modern conceptions of the anatomy of the Trilobite limb are based, but he has given no reasons, beyond Walcott's beautiful photographs, in support of his view that the endopodite and exopodite should be reversed. We are not in a position to judge of the relative merits of the observations on which the two opposed views are based, but we feel that we must assume that the view based on the observations of the actual specimens is more likely to be the correct one. However, in a reply to a paper by RICHTER (1926) (a paper incidentally the value of which as a criticism is greatly diminished by the inaccurate statements that it contains), STORCH (1926) has put forward his conceptions as to the mode of life of the Trilobites, and on these points we are in complete disagreement with him. He has deduced that the Trilobites, instead of being, as originally supposed, bottom living forms that crawled on the inner ramus of the limb but could also swim with the outer ramus, were really swimming forms like the modern Anostraca. He states (1926, p. 154): "Ich muss auch weiter auf meiner Ansicht verharren, dass die Trilobiten bloss schwimmende Fortbewegungsweise besaßen." His first point is that among the Crustacea there is



TEXT FIG. 13.—Diagram representing the suggested evolution of the Anostracan type of limb from a primitive biramous type.



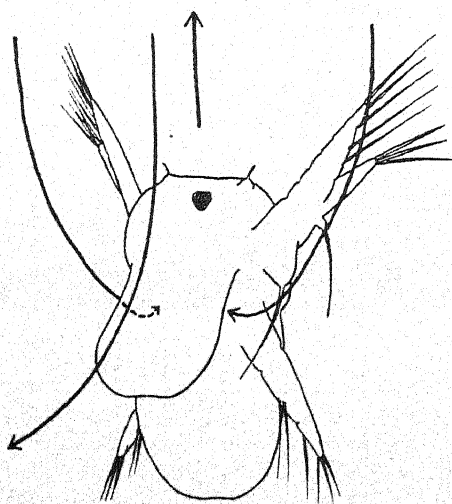
no single case where the endopodite and the exopodite are adapted, the one for walking, the other for swimming, "immer sehen wir die Differenzierung nur in der Art durchgeführt, dass eine Anzahl von Beinpaaren zum schreiten, eine andere Anzahl von Beinpaaren zum Schwimmen verwendet wird." This, however, is not so. Some mysids, for instance *Macromysis inermis*, and many larval forms such as Euphausiid larvæ, can walk on the endopodites of their thoracic limbs while the exopodites are swimming organs. The second antenna of certain Ostracods can also be used for crawling or for swimming. The second point deals with the rhythmical movement which it is supposed was exhibited by the Trilobite limbs. He states: "Richter selbst sagt (p. 309), 'Die Bewegung der Beine vollzog sich in wellen.' Aber eine rhythmische Bewegung in diesen Sinne kann wohl niemals eine Schreitbewegung sein." Unfortunately, he does not give any reasons why rhythmical movement of pediform limbs cannot result in walking movement. Surely this is the normal method of progression in millipedes. It is also by a rhythmical movement of the ribs of a snake that it is enabled to move when coiled up in the branches of a tree. But even in such a common form as a lobster the trunk limbs move rhythmically. In fact, when limbs are numerous, a co-ordinated rhythmical movement is necessary for the stability of the body. His third point is that nowhere among the Crustacea are flat, unjointed, foliaceous limbs (*Turgorextremitäten*) primarily swimming organs. These are always powerful jointed limbs (*Skelett-textremitäten*); witness the second antennæ of Cladocera, etc. He admits that such foliaceous limbs may be swimming organs, e.g. in Anostraca and Notostraca, but in these cases this is a secondary function. He puts forward the view rather that the pediform branch of the Trilobite limb, p. 156, "der kräftig und unbehindert ins Wasser hinein wirken kann," represents the swimming portion of the limb, the foliaceous branch acting as a food gatherer and at the same time supporting the pediform branch. Exactly how the two branches of the limb worked together he does not explain; but, if his contention is correct, it appears to us purposeless to distinguish either branch specially as the swimming organ. If they do work together "*in engster Koppelung*" (p. 156), the pediform branch would provide the motive power of the swimming stroke, while the foliaceous branch would offer the large surface of resistance to the water; that is, the former would act as the handle of the oar, the latter as the blade.

Thus, if we have understood STORCH correctly, the first two main points that he adduces in support of his views we consider based on incorrect observations. The third point, we think, results from a faulty comparison. He states that the swimming limbs of Crustacea are always powerful, many-jointed *Skelett-textremitäten*. He quotes as examples (p. 156) the second antennæ of the Cladocera, the second antennæ of the Ostracoda, and the thoracic legs of the Copepoda. Now, the first of these are biramous limbs provided with many laterally projecting feathered setæ, so that the whole limb possesses a very large surface of resistance when spread out like a fan during the swimming stroke. The antennæ of the Ostracoda, when they are actually swimming and not creeping organs, are provided with a tuft of long setæ which again offer a large surface of resistance to the water. The thoracic legs of the Copepoda are also provided with margins of fringed setæ; and in any case, if these do show relationship to any one known Crustacean limb more than to another, it is to the foliaceous type rather than to the pediform type, as the discovery of *Lepidocaris* has demonstrated. Thus, these three examples that STORCH has quoted do not appear to us to show any special resemblance to the pediform branch of the Trilobite limb. They are simply markedly jointed as opposed to the foliaceous type, and there the resemblance ends. However, STORCH states further that among the Malacostraca there are many swimming limbs similar to the pediform branch of the Trilobite limb. But are there? We do not know of any unfringed pediform

limb among the Malacostraca that is used for swimming, but, on the contrary, we can name many examples of pediform limbs that we know actually to be used for walking, and these bear a strong resemblance to the pediform branch of the Trilobite limb, as an example at random, the posterior thoracic limbs of most Decapoda. To assume that a simple pediform limb was used for swimming appears to us contrary, not only to the observed facts of comparative carcinology, but also to the general principles upon which the swimming power of aquatic organisms is based. If a limb is to be used for swimming it must somehow, by branching or feathering or otherwise, offer a comparatively large surface of resistance to the water, and this applies especially to the limbs of such massive forms as the Trilobites.

We consider, then, that STORCH has not put forward any case that will stand criticism in support of the idea that the pediform branch of the Trilobite limb was natatory in function, and we accept the general view that it was the ambulatory branch of the limb. Assuming this, there appears to us no reason for the reversal of the homologies of the branches of the limb. The Trilobites, according to our views, arose, just as did the Branchiopoda, from a primitive form in which the limbs were all similar and biramous. But whereas in the ancestors of the Crustacea they were primitively arranged in a parallel series, in those of the Trilobita they projected laterally from the sides of the body.

The primitive Trilobites (DOLLO, 1909) most probably led a life similar to that of *Limulus*; that is, they were crawling littoral forms, and it is reasonable to suppose that their ancestors were also bottom-living forms. We consider it is possible that the food-collecting mechanism arose automatically with the foliaceous appendages developed in correlation with swimming tendencies (see next section). The process of food-gathering resulted simply from the eddy currents that we have demonstrated must exist up the faces of any flat oscillating limbs.



TEXT-FIG. 14.—Oblique side view of an Estherid nauplius. The upper arrow indicates its direction of motion. Of the other arrows, the middle represents the current of water forced away from the axis of the body by the large projecting labrum, the others indicate the currents of water sucked in behind the labrum into the mouth region.

These would lead a food stream up to the bases of the limbs; but, since the limbs were not close together, their motion would not cause a current in the ventral food groove, and so there must have been some other mechanism for drawing the currents from the bases of the limbs to the mouth. This was provided by a large labrum. Such a large ventrally projecting labrum, we have already explained, would suck in water to the mouth region; and hence the food currents reaching the base of the limbs, and more especially those associated with the anterior limbs, would be sucked forwards to the mouth. Now, such a form as this is not hypothetical. It is to be found in *Marella*. In this form the axes of the limbs projected laterally from the sides of the body. The exopodites were foliaceous and the endopodites were obviously adapted for crawling, and there were as yet no gnathobases. But, in addition, *Marella* possessed a large ventro-posteriorly projecting labrum.

The existence of the large labrum, not only in *Marella* but in practically all nauplii (text-fig. 14) and in many modern Phyllopoda, is very significant. We suggest that in the primitive articulate ancestor from which both the Trilobita and Crustacea arose, it was through the "passive" activity of the labrum sucking food into the mouth region that the animals fed. By crawling over the bottom by the

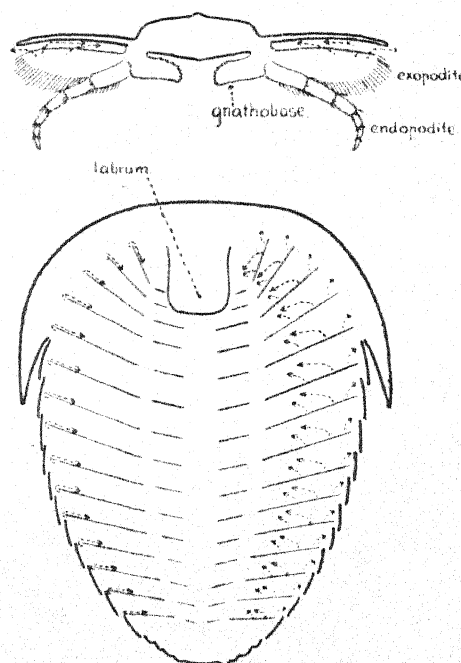
inner branches or merely the inner portions of its appendages, it would disturb the bottom detritus, and this would then be automatically sucked into the mouth region. The development of the outer portions of the appendages as swimming organs to assist progression would lead to such a form as *Marella* with a secondary food-gathering mechanism.

The Trilobites, according to our views, evolved from forms which possessed a feeding mechanism similar to that of *Marella*. The advance shown in the Trilobite constitution is in the possession, firstly, of the well-developed pleural shield closely covering the exopodites, and, secondly, of gnathobases on the trunk limbs. The latter clearly developed as a mechanism for assisting the food forwards from the base of the limbs to the mouth. The pleural shield, we believe, developed as a structure which would increase the efficiency of the exopodites as food gatherers. As we explained above (p. 243), the presence of a flat plate near to a vibrating limb would suck towards the base of the limb the backwash around the sides of that limb nearest to the plate. Thus the backward motion of the exopodites close underneath the pleural shields would cause a backwash passing obliquely across the limbs between them and the pleural shield, and this is, of course, a current in an oral direction (text-fig. 15).

It is possible that in *Lepidocaris* the peculiar scale-like plates that "protect" the bases of the trunk limbs also represent structures analogous to the pleura of the Trilobites, and developed in correlation with the same needs.

We have summarised our views as to the evolution of the various types of "filter-feeding mechanism" in text-fig. 16. We have started from a primitive articulate form that possessed simple biramous appendages, projecting, as in most annelids, in a ventro-lateral direction. From this point there are two main lines of evolution: on the one hand, in any segment the limbs project ventrally and parallel to each other, and this leads to the modern Branchiopod type; while, on the other hand, the limbs project laterally, and this leads to the Trilobite type.

As to the origin of the feeding mechanism of the primitive Malacostraca, and more especially of that of *Hemimysis*, we feel that we cannot make any critical suggestion, for the simple reason that the common ancestor of the various Malacostracan orders was itself a very highly specialised Crustacean, and we have very little evidence to indicate how it was evolved from the more primitive forms. However, CALMAN, in his list of "caridoid facies," includes as the primitive trunk limb a limb which does not differ materially from that of *Hemimysis*, and it is reasonable to suppose that in this ancestral form it was used in the same way as in *Hemimysis*. The ancestral Malacostracan would thus be a form in which the limbs immediately behind the mouth were highly specialised for feeding, while the trunk limbs were primarily both swimming and crawling organs with a secondary function of collecting food. *Lepidocaris* and the



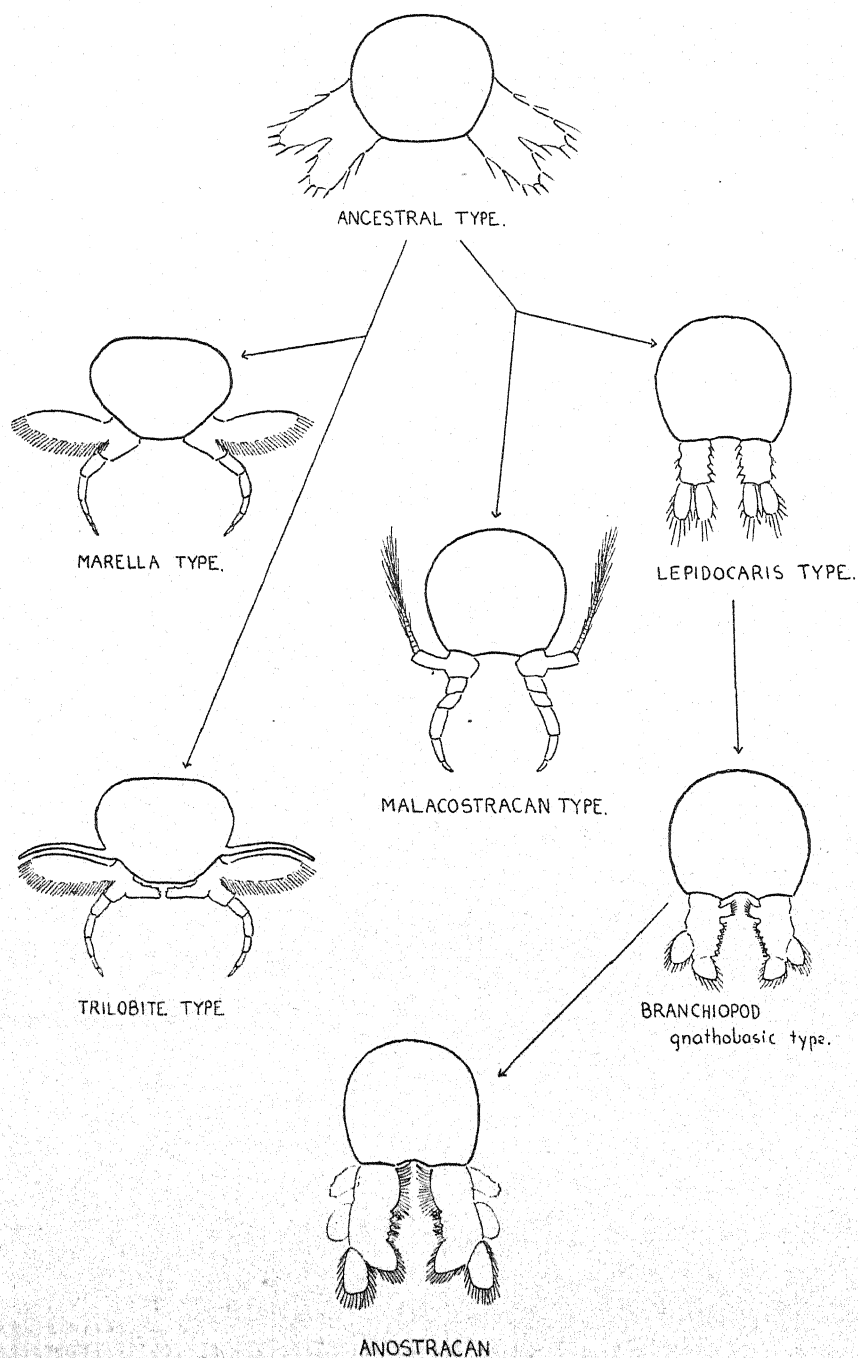
TEXT-FIG. 15.

FIG. 15a.—Diagrammatic cross-section of a typical Trilobite, showing the backwash feeding currents caused by the exopodites immediately underneath the pleura.

FIG. 15b.—Diagram of a typical Trilobite, showing the currents caused by the back stroke of the exopodites. The position of the limbs is indicated by the continuous straight lines. The shorter lines towards the middle represent the gnathobases. On the left of the figure the dotted lines represent the eddy currents up the anterior faces of the exopodites. On the right are indicated the backwash currents produced between the exopodites and the pleura.



Branchiopoda on the one hand, and Marella and the Trilobita on the other, evolved in correlation with the same habits, namely, the tendency of the bottom-living, articulate, adult ancestor to swimming activities, a tendency which would lead it to new environment and new food.



TEXT-FIG. 16.—Diagram summarising the suggested evolution of the various types of feeding found in the Crustacea and Trilobites.

The Malacostraca probably evolved in the same way, but only after the anterior limbs immediately behind the mouth had become specialised into an elaborate feeding mechanism involving a true filtering process. In Lepidocaris and the Branchiopoda the swimming functions devolved mainly on the endopodite; while in the Malacostraca, as in Marella and the Trilobita,

it was the exopodite that became the main swimming organ. In the Malacostraca, however, a foliaceous exopodite was not evolved, but, instead, a multiarticulate brush-like structure. Such a structure would not, by simple oar-like action, produce the food-collecting eddy currents that we have demonstrated must exist with a foliaceous limb; but a change from a simple backwards and forwards oar motion to a rotatory motion such as occurs in *Hemimysis*, would lead to the production of the food-collecting swirls without at the same time impairing the efficiency of the limb as an oar.

#### SUMMARY.

1. *Hemimysis lamornæ* exhibits two distinct types of feeding, the one on large food masses and the other on minute suspended particles filtered from a water current.

2. In the filter-feeding mechanism the maxilla acts both as a suction-pump and as a true filter. By its vibration it sucks forward a food-bearing stream of water from the ventral food groove. This suction is aided by an exhalent respiratory current produced by the epipodite of the first trunk limb. The comb of setæ on the proximal endite of the maxilla forms the filtering plate. The exit for the filtered food stream lies between the maxillary exite, the maxillule, and the body wall. The food collected in the food groove and on the filtering combs is pushed on to the mouth between the bases of the paragnaths by the long setæ on the proximal endites of the maxillules, one long seta on the proximal endite of the maxillæ, and the comb of setæ on the proximal endites of the first trunk limbs. It is pushed directly on to the spine-rows of the mandibles.

3. The food stream along the ventral food groove is produced by the swimming activities of the exopodites of the thoracic limbs. Each exopodite rotates so that its tip describes an ellipse. Its setæ are so placed that when it is passing backwards they become spread out, while on passing forward they collapse; the exopodites thus propel the animal forwards on their backward strokes. By this rotatory action a food-bearing stream is sucked down each cone of rotation and passes in between the bases of the trunk limbs to the ventral food groove.

4. Large food masses are held by the thoracic endopodites and mandibular palps, the latter being used chiefly to adjust the food mass over the mouth-parts. The food mass is bitten into by the incisor processes of the mandibles, aided by the distal endites of the maxillules. The mandibles are asymmetrically arranged so that the food bitten off by the incisor processes is automatically passed on to the *lacinix mobiles* and then to the molar processes.

5. We have criticised STORCH's description of the feeding process of *Daphnia* and his views on the evolution of the feeding mechanism of the Crustacea and Trilobites.

6. While STORCH considers the primitive Crustacean feeding limb to have been a phyllopodium similar to that of the modern Anostraca, and functioning essentially as a filtering mechanism, we suggest that the primitive limb was a simple biramous paddle such as occurs in the posterior trunk segments of *Lepidocaris*. These limbs functioned primarily as swimming organs, and in their effective back stroke produced backwashes towards the bases of the limbs and towards the mouth which constituted the main food stream.

7. From primitive articulates possessing biramous limbs we consider that, on the one hand, the Branchiopoda and other Crustacea evolved from forms in which the limbs projected ventrally from the body in two parallel series, while, on the other, Marella and the Trilobites arose from forms in which the limbs projected laterally.

8. Among the Crustacea the endopodite became a foliaceous swimming organ in the Branchiopoda, while in the Malacostraca it was the exopodite which developed as the swimming part of the limb, but in this case it became "whip-like" and not foliaceous. In both cases

the swimming activities produced an orally directed food stream. In the Branchiopoda this food stream is enhanced by the presence of a large labrum with well-developed labral glands. In the Malacostraca the maxillæ form a true filtering mechanism which sucks forwards the food stream produced by the more posterior limbs.

9. In Marella and the Trilobites the exopodite became the swimming branch of the limb. In Marella these exopodites, together with a very large labrum, formed the feeding mechanism. In the Trilobites we consider that the pleural shield developed to enhance the food-collecting activities of the trunk limb exopodites.

10. Our suggestions as to the functioning of the Trilobite limbs are based on the usually accepted homologies of the two branches of the limbs, and do not involve the "reversal" of the endopodite and exopodite, as suggested by STORCH.

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## LIST OF ABBREVIATIONS USED.

<i>a. 1.</i>	antennule.	<i>mx. 1 d.</i>	distal endite of maxillule.
<i>a. 2.</i>	antennal flagellum.	<i>mx. 1 p.</i>	proximal endite of maxillule.
<i>a. 2. sc.</i>	antennal scale.	<i>mx. 1 sp.</i>	long spines from the proximal endite of the maxillule.
<i>bas.</i>	basipodite of thoracic limb.	<i>mx. 2.</i>	maxilla.
<i>c.</i>	carapace.	<i>mx. 2 p.</i>	proximal endite of maxilla.
<i>e.</i>	eye.	<i>mx. 2 d.</i>	divided second endite of maxilla.
<i>e. pl.</i>	endoskeletal plate.	<i>mx. 2 ex.</i>	exite of maxilla.
<i>ex.</i>	exopodite.	<i>mx. 2 pl.</i>	maxillary palp.
<i>f.</i>	ventral ectodermal attachment to mandibular tendon.	<i>oes.</i>	oesophagus.
<i>f. bas.</i>	food basin.	<i>p.</i>	paragnath.
<i>f. gr.</i>	food groove.	<i>p. b.</i>	paragnath base.
<i>f. gr. p.</i>	posterior entrance to food groove between the eighth basipodite and the penis.	<i>pe.</i>	penis.
<i>g.</i>	median muscle to food groove from the endoskeletal plate.	<i>pl.</i>	pleopod.
<i>inc.</i>	mandibular incisor process.	<i>r. l.</i>	spined posterior ridge of labrum on left side.
<i>lac. r.</i>	right mandibular lacinia mobilis.	<i>r. r.</i>	spined posterior ridge of labrum on right side.
<i>lac. l.</i>	left mandibular lacinia mobilis.	<i>sp. r.</i>	right spine-row of the mandible.
<i>lbr.</i>	labrum.	<i>sp. l.</i>	left spine-row of the mandible.
<i>mdb.</i>	mandible.	<i>sp. f.</i>	spines on floor of upper oral cavity.
<i>mdb. p.</i>	mandibular palp.	<i>th. end.</i>	thoracic endopodite.
<i>mdb. t.</i>	tendon of mandibular adductor muscles.	<i>th. 1 c.</i>	proximal endite of first thoracic limb.
<i>mol.</i>	molar process of mandible.	<i>th. 1 end.</i>	first thoracic endopodite.
<i>mol. l.</i>	left molar process.	<i>th. 2 bas.</i>	second thoracic basipodite.
<i>mol. r.</i>	right molar process.	<i>th. 2 end.</i>	second thoracic endopodite.
		<i>2a, 2b, etc.</i>	levels of sections in text-figures 2a, 2b, etc.
		<i>8a, 8b, etc.</i>	levels of sections in text-figures 8a, 8b, etc.

## DESCRIPTION OF PLATES.

## PLATE I.

Fig. 1. Ventral view of head and thorax with the third to eighth endopodites of the right side removed, the mouth-parts being visible on the right side.

## PLATE II.

Fig. 2a. Inner view of one-half of an animal which has been divided sagittally, showing the mouth-parts.

## PLATE III.

Fig. 2b. Enlarged portion of the above, with the first trunk limb removed, its position being indicated by the dotted line.

Fig. 3a. Posterior view of the biting edges of the mandibles and the lower edge of the labrum.

Fig. 3b. Spine from left edge of labrum.

Fig. 3c. Spine from right edge of labrum.

Fig. 4. Posterior view of mouth-parts from behind the maxillary segment; the left maxillule is removed.

## PLATE IV.

Fig. 5. Ventral view of mouth-parts; the first trunk limbs and right maxilla are removed. The position of the endopodite of the first trunk limb is indicated by the dotted line, but the spines are only shown on the proximal arrows.



H. GRAHAM CANNON and Miss S. M. MANTON "On the Feeding Mechanism of a Mysid Crustacean,  
*Hemimysis Lamorea*." PLATE I.

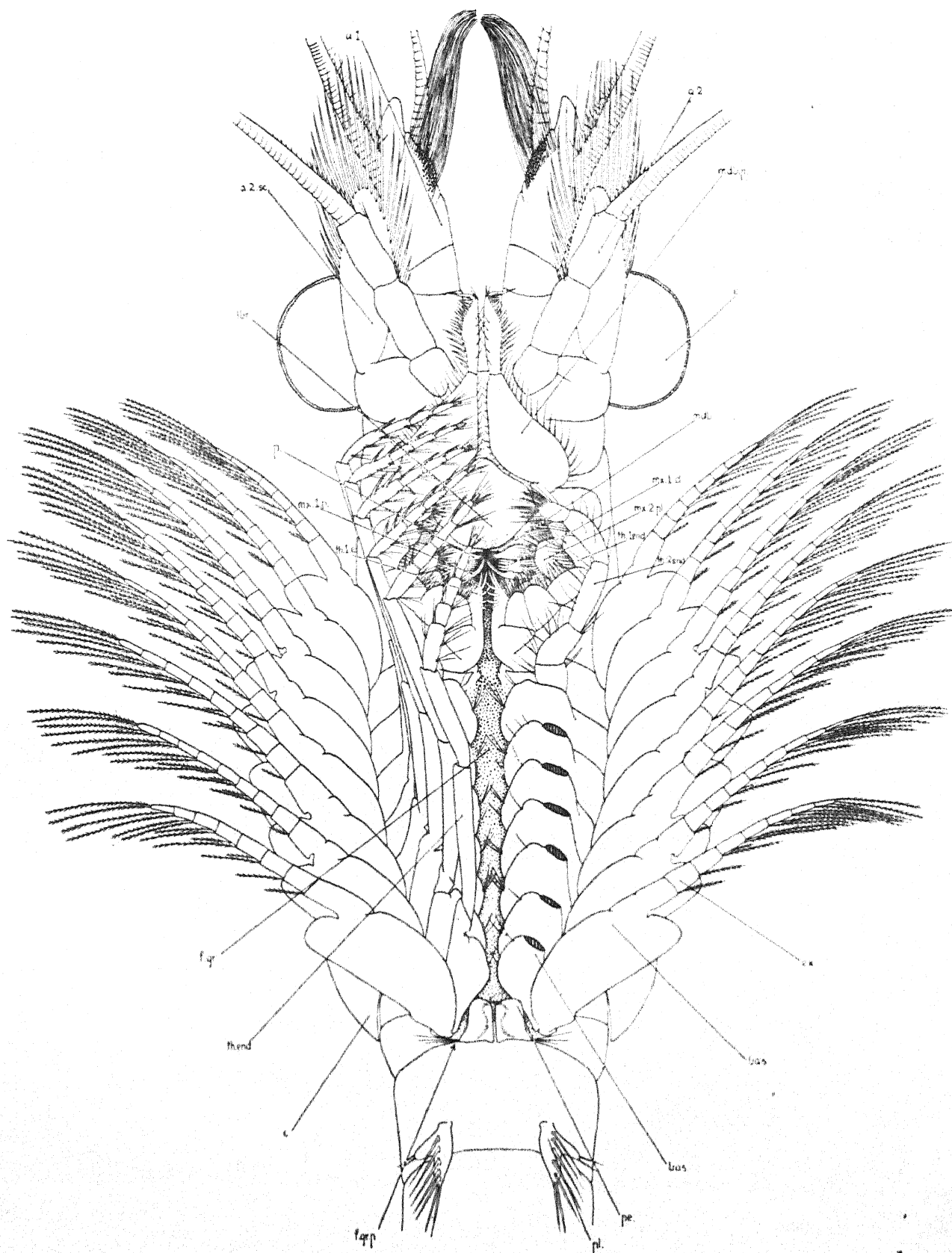


FIG. 1.  $\times 34$ .





H. GRAHAM CANNON and Miss S. M. MANTON "On the Feeding Mechanism of a Mysid Crustacean, *Hemimysis Lamornæ*." PLATE II.

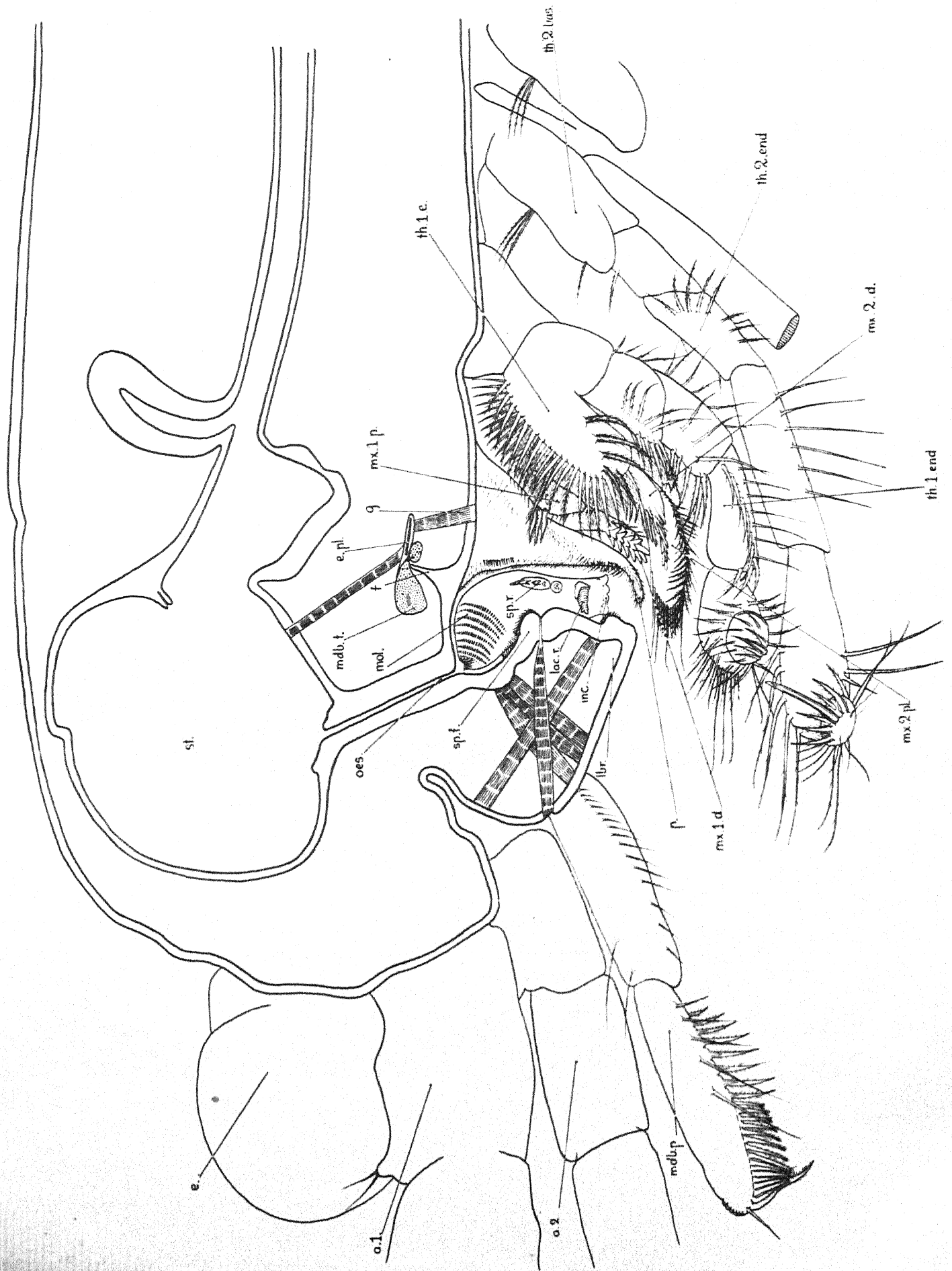


FIG. 2a. X 96.





H. GRAHAM CANNON and Miss S. M. MANTON "On the Feeding Mechanism of a Mysid Crustacean, *Hemimysis Lamornei*." PLATE III.

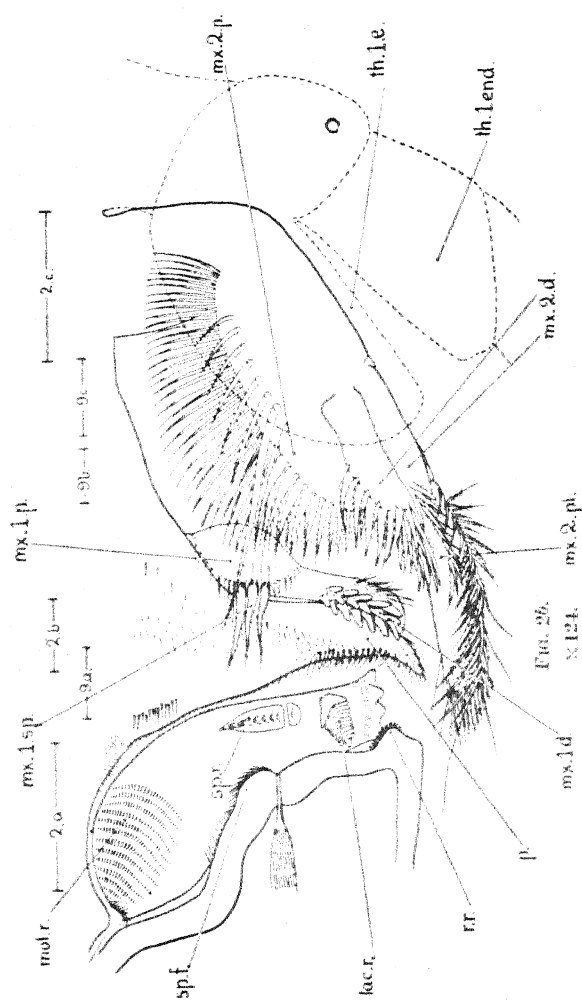


FIG. 2b.  
× 124.

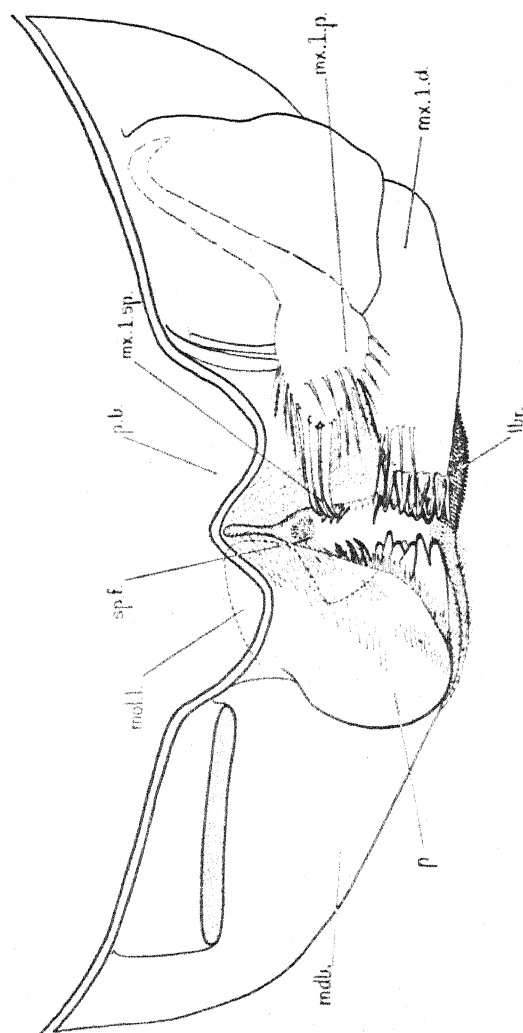


FIG. 4. × 100.



FIG. 3b.



FIG. 3c.

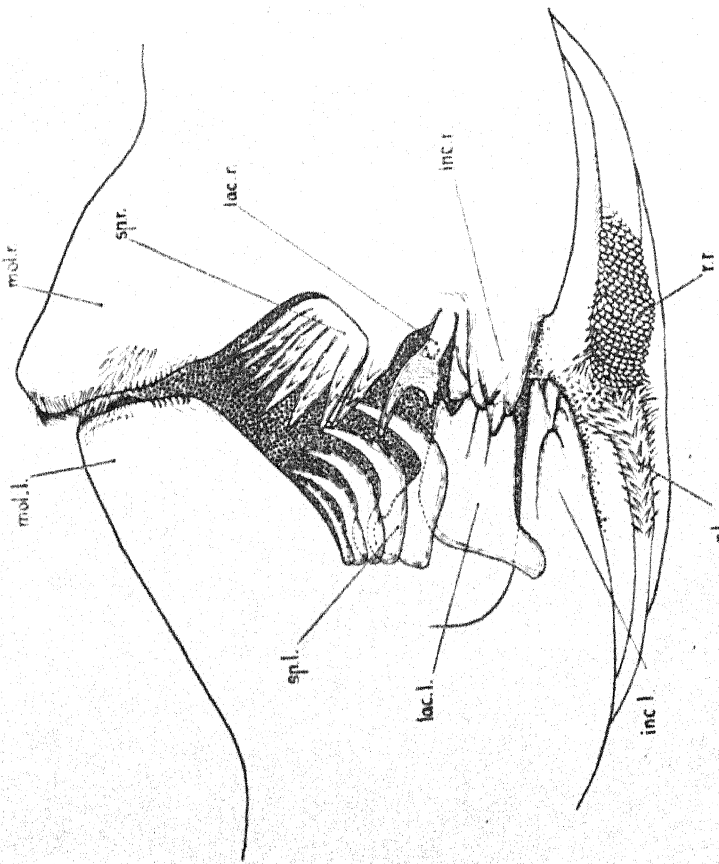


FIG. 3a. × 250.



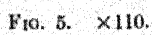


FIG. 5.  $\times 110$ .





XI.—The Fish-Fauna of the Cementstones of Foulden, Berwickshire. By Errol Ivor White, of the British Museum (Nat. Hist.). Communicated by Professor W. T. Gordon, D.Sc. (With Forty-six Text-figures.)\*

(MS. received December 1, 1926. Read January 10, 1927. Issued separately May 20, 1927.)

So barren of fossil remains is the Cementstone Group of the Scottish Lower Carboniferous Rocks that any addition to our knowledge of the fauna and flora of the period is especially welcome. The list of vertebrate remains is notably meagre, and such as have been found, *e.g.* at Abden, are generally very fragmentary.

The collection to be described below contained nearly 150 specimens, and includes Plants, Lamellibranchs, Amelids, Arthropods, and Fishes: of these the Plants and Fishes are by far the most important, and constitute more than two-thirds of the total number of specimens.

All the specimens were obtained from sections exposed in the Crooked Burn, 50 yards below Newton Farm in the parish of Foulden, 5 miles west of Berwick-on-Tweed.

The beds in which the remains were found belong to an horizon quite near the base of the Cementstones, and consequently the fauna is one of the earliest known from Lower Carboniferous Rocks.

The lithology of the beds is somewhat inconstant, in a manner typical of these shallow-water deposits: all are argillaceous and highly charged with lime. The rock in the majority of cases is a fine-grained, somewhat sandy shale, and contains a fair sprinkling of mica. In a few instances the sandy element is coarse and predominates, while in others it is wanting, and the rock is a very fine-grained, horny, mudstone with conchoidal fracture. The series is, therefore, typically estuarine in character.

The area has been neglected geologically since 1864, when it was surveyed by ARCHIBALD GEIKIE (GEIKIE, 1864). At that time, no specifically identifiable fish-remains were found except rhizodont scales: indeed, to judge from SALTER's list, few of the organic contents of these strata seem to have been sufficiently well-preserved for complete identification (SALTER, 1864). The fossils now to be described vary much in their state of preservation. The lamellibranchs have suffered most and are scarcely recognizable, being for the most part in the form of distorted casts: the arthropods also are rather broken, and in the case of those preserved in the more sandy layers the delicate remains have tended to flake off. The plants have suffered in the usual manner of drifted material, but the heavily armoured fishes are mostly in a fine condition. All are compressed and flattened, usually laterally, and in most only the external features are available for study: nevertheless a few of the fishes do show something of their internal anatomy.

These fishes are interesting in that the small and more complete forms are new, and it has been necessary to erect four new genera for their reception: but the larger forms, represented by teeth, scales, and other isolated fragments, belong to predatory fishes of well-known and widely distributed species.

This fine collection owes its existence to the zeal of the late THOMAS MIDDLEMISS OVENS, an enthusiastic young local geologist, and the state of the specimens is a tribute to his careful and skilled collecting. It is greatly to be deplored that Mr OVENS' activities have been cut short by his untimely death at the age of nineteen.

\* Published by permission of the Trustees of the British Museum.

Mr and Mrs JOHN OVENS, of Foulden, have generously presented their son's collection to the British Museum, where all the specimens described here are now preserved. The majority of the plants, however, had been sent to the late Dr KIDSTON during the lifetime of the collector, and are now in the Jermyn Street Museum. They are partly described in the *Memoirs of the Geological Survey of Great Britain (Palæontology, vol. ii, 1923-26)*, and a note on the specimens in the British Museum is here appended; for this I am indebted to my colleague Mr W. N. EDWARDS.

My best thanks are due to Sir A. SMITH WOODWARD, Professor D. M. S. WATSON, and Professor W. T. GORDON for much help and advice. I am further indebted to Professor GORDON for acting as sponsor to this paper, and I would also like to express my sense of gratitude to Dr T. M. FINLAY for the trouble taken in preparing slides and an abstract which he communicated to the Society, and to Miss B. A. MORTLEMAN for her careful preparation of the manuscript.

Sub-class "SELACHII."

Order ACANTHODII.

Family ACANTHODIDÆ.

Genus ACANTHODES, Agassiz.

*Acanthodes ovensi*, sp. nov.

(Text-figs. 1-3.)

*Specific Characters*.—A small *Acanthodes* attaining a length of 9-10 cm. (proportions doubtful): caudal pedicle very stout, its depth at hinder end exceeding one-half distance from anal fin-spine to commencement of lower caudal lobe. Fin-spines gently arcuate with a single groove running near to, and parallel with, the anterior border. Pectoral fin-spine relatively short and broad; other spines more slender. Ventral spine rather longer than half the pectoral and situated nearer to it than to the anal, the distances being approximately as 2:3. Dorsal and anal spines about equal in length and (apparently) but little shorter than the pectoral; dorsal fin-spine inserted opposite, or slightly anterior to, the anal. Scales smooth or with slight median pit.

*Holotype*.—Imperfect fish, Brit. Mus., P. 13137.

*Paratypes*.—Six specimens, Brit. Mus., P. 13136, P. 13138-P. 13142.

*Description of Specimens*.—The seven specimens by which this species is known are all imperfect and only one, the holotype (text-fig. 1), is fully grown.



TEXT-FIG. 1.—*Acanthodes ovensi*, n. sp. Holotype. [P. 13137.  $\times 1$ .]

The holotype is almost complete but telescoped in the region of the head and shoulders, and the tip of the tail is missing. Of the others, P. 13138 is fairly complete, but the outlines of the anterior part are indistinct; P. 13136 is an imperfect anterior portion; P. 13140 is crushed dorso-ventrally and lacks the tail; the remainder are the posterior portions of small fishes of which P. 13139 and P. 13141 are moderately well-preserved.

*Shape and Size*.—Unfortunately no specimen shows a clear and undistorted view of the anterior half of the body. The holotype itself (text-fig. 1) is not only foreshortened in the head region, but deepened by crushing, and the three other specimens which possess a head are



dorso-ventrally flattened in front and show the ventral aspect only. The inconstancy of the position in which these fishes are preserved indicates that they were round-bodied.

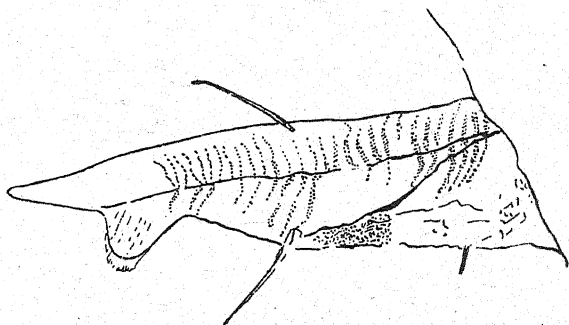
The caudal pedicle is notably short and stout (text-fig. 2, P. 13141) and the fish does not appear to have been so slender in its general proportions as the majority of the species of *Acanthodes*.

The holotype must have been between 9 and 10 cm. in length when alive, but with the exception of the crushed specimen, P. 13140, the others are the remains of very small fishes: indeed, P. 13139 (text-fig. 2), and P. 13141 could scarcely have exceeded 3.5 cm. in total length.

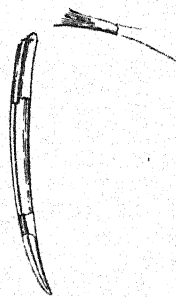
**Myotomy.**—In most of the specimens the myotomy is discernible owing to the rucking up of the skin. It is best seen in P. 13139 (text-fig. 2) in which 25 myotomes are to be counted in the posterior half, and in P. 13138 about 40 are visible.

**Skull.**—In the holotype the skull is crushed and shapeless.

**Visceral Skeleton.**—Besides the scarcely decipherable fragments of the jaws seen with the skull in the holotype, the only remaining portions of the visceral skeleton are parts of the



TEXT-FIG. 2.—*Acanthodes oveni*, n. sp. Small individual showing Myotomy. [P. 13139.  $\times 3$ .]



TEXT-FIG. 3.—*Acanthodes oveni*, n. sp. Pectoral fin-spine. [P. 13140.  $\times 3$ .]

branchial arches with their long and slender supports for the dermal gill-flaps (P. 13136, 8, 40).

**Skeleton of the Unpaired Fins.**—The fin-spines alone represent the skeleton of the dorsal and anal fins. They are narrow and gently arcuate, and of approximately the same length, which is about equal to the body depth at their insertion. A longitudinal groove runs near to the anterior border.

The dorsal fin-spine is far forward in position and is opposite, if not actually anterior, to the anal spine. In P. 13140 these spines, although well-preserved, are reversed in relative position owing to the crushing of the body.

The caudal fin is quite typical and calls for no special comment.

**Skeleton of the Paired Fins.**—Only the proximal end of the pectoral fin-spine is preserved in the holotype, and to this is attached the usual elongated dumb-bell shaped element; no other structures are preserved in any specimen. The support is very long and slender; it measures upwards of 6.0 mm. in P. 13137, and exceeds one-half the length of the spine itself in P. 13140. The pectoral fin-spines are broader, but not much longer than those of the median fins. In only one specimen, P. 13140 (text-fig. 3), is the whole spine preserved, and in this case it measures 11.5 mm. while the dorsal spine is a little over 10.0 mm. long.

The ventral fin-spines are narrow but relatively long, and that in the specimen quoted above (P. 13140) measures 6.5 mm., or more than one-half the length of the pectoral spine.

These spines lie nearer to the last-named than to the anal fin; the distances being roughly in the proportion of 2 : 3 (P. 13138).

The paired fin-spines are decorated in the same manner as those of the median fins.

Squamation.—The body is covered with the usual quadrate scales, which are smooth, or have a faint median pit and a very convex and smooth inner face. Those along the belly, especially in the region of the anal fin, are very much smaller than the flank-scales; and of the latter the more posterior are the larger. This variation in size is not peculiar to the species, as it is seen in specimens of *A. sulcatus* (P. 11292) and *A. bronni* (No. 33060) as described by AGASSIZ (1833, p. 19).

The scales, as usual, are much smaller on the caudal lobes, and the rows bifurcate in the normal fashion. None is seen on any of the other fins.

Lateral Line.—This is conspicuous in P. 13138-9 and to a limited extent in the holotype, but no details of its structure are preserved.

Remarks.—The distinctive features of this species are the short, stout, caudal pedicle and the anterior position of the dorsal fin. These are sufficient to separate it from the more perfectly known of the Lower Carboniferous forms (WOODWARD, 1891, *A. nitidus* and *A. sulcatus*), and it differs from *A. striatus* in the smoothness of the scales (WELLBURN, 1901). It is fairly typical of the Lower Carboniferous species in respect of the relative shape and position of its paired fins (WOODWARD, 1891, p. 5), but the ventrals are rather more anteriorly placed than usual. Only one other species of *Acanthodes* has the dorsal spine so far forward, and this, *A. parvulus* from the Permian of Siberia, is imperfectly described, but the unpaired fin-spines are apparently shorter (ROHON, 1889, p. 7).

#### Family GYRACANTHIDÆ.

Genus GYRACANTHUS Agassiz.

*Gyracanthus* sp. indet.

There are two fragments (P. 13122-3) referable to this genus in the collection, but neither is specifically determinable.

#### Order EUSELACHII.

Family PETALODONTIDÆ.

Genus CALLOPRISTODUS, Traquair.

*Callopristodus pectinatus* (Agassiz).

P. 13125, the only specimen of this species from Foulden, is the impression of a typical tooth.

Sub-class TELEOSTOMI.

Order CROSSOPTERYGII.

Family RHIZODONTIDÆ.

Genus RHIZODUS, Owen.

*Rhizodus hibberti* (Agassiz and Hibbert).

Scales of *Rhizodus* are not uncommon, P. 13129-13134 being typical examples. They are thinner than those of *R. ornatus* Traq., and show the fine granulations on the exposed area seen in the larger species. All except P. 13133a are quite small, but there is a large fragment measuring 4.5 cm. across, which shows the inner boss.



P. 13135 comprises the greater part of an operculum similar in shape to those of *R. ornatus* in the British Museum, e.g. P. 3322a, but differing considerably from a specimen, 21975b, which is referred to the genotype by SMITH WOODWARD (1891, p. 344). It is perfectly smooth. Some fragmentary fin-rays may also belong to a fish of this genus.

Genus STREPSODUS, Young.

*Strepsodus* cf. *sulcidens* (Hancock and Atthey).

Two teeth, P. 13127-8, are very similar to those of the well-known Coal Measure species. The first example has been cleaned of matrix, but the second lies in a piece of rock typical of the sandier facies of the fish-bearing beds. The roundness of the cross-section of these teeth precludes the possibility of their reference to *Rhizodus*, while the upward extension of the basal furrows and the elongated but robust form are typical of *S. sulcidens*. The specimens are, however, smoother than is usual in that species and lack the fine vertical striæ on the inner face; and on that account, coupled with their geological horizon, their systematic position must be regarded as somewhat uncertain.

*Strepsodus striatulus* Traquair.

There is one imperfect but typical tooth in the collection (P. 13124).

*Strepsodus* sp. indet.

A much broken and worn scale (P. 13126) shows the characteristic longitudinal furrows of the exposed surface. It is not specifically identifiable.

#### Order ACTINOPTERYGII.

##### Family PALÆONISCIDÆ.

##### Genus FOULDENIA, nov.

Trunk elongately fusiform. Suspensorium oblique but gape small. Operculum small, equalled or exceeded in size by suboperculum; anterior expansion of preoperculum deeper than long and bent at right-angles to lower limb. Posterior expansion of maxilla triangular. Jaws stout and obliquely placed; some teeth of lower jaw blunt and tumid. Bones of head and opercular apparatus ornamented with rugæ and tuberculations; mandible and oral margin of maxilla smooth with longitudinal grooves, irregular in the lower jaw. Fins well developed with large anterior fulcral rays still attached to base; rays of median fins numerous, articulated throughout, and distally dichotomized (state of rays of paired fins unknown). Dorsal fin with extended base and origin opposite or slightly anterior to ventral fins; anal fin also long-based and both fins triangular in shape with maximum depth far back, the anterior rays being graduated. Caudal body prolongation long and attenuated, the fin only slightly forked, inequilobate. Scales of moderate thickness, covered with ganoine. Much enlarged median ridge-scales run from occiput to dorsal fin and from dorsal and ventral fins backwards, those behind dorsal and anal fins being very long and slender.

This genus contains only one known species:—

*Fouldenia ottadinica*, \* sp. nov.

(Text-figs. 4-13.)

*Holotype*.—Imperfect fish, Brit. Mus., P. 13178.

\* Named after the Ottadini, an ancient British tribe inhabiting this part of Berwickshire at the time of the Roman Occupation.

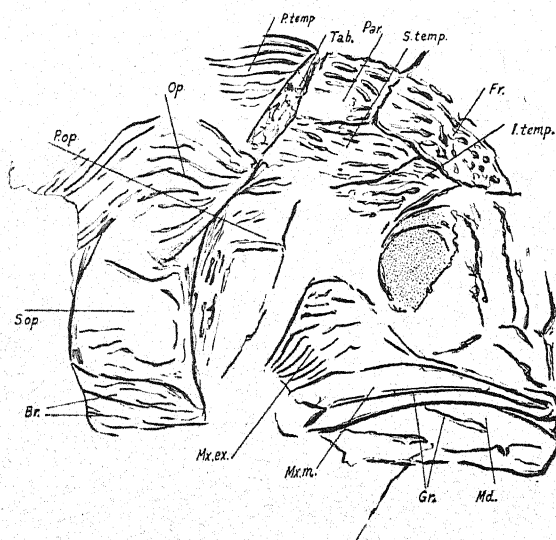


*Paratypes*.—Eight specimens, two in counterpart, Brit. Mus., P. 13179–P. 13183, P. 13185–P. 13188.

*Description of Specimens*.—None of the specimens is complete, but collectively they show nearly all the characters of the genus.

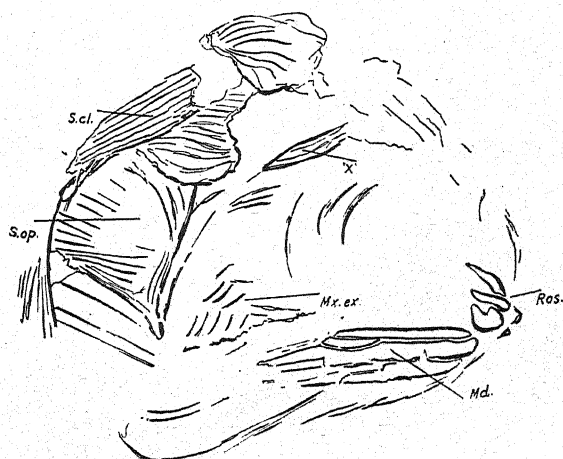
The holotype shows the most details, including the external characters of the head, the shape, squamation and portions of the pectoral, anal, and caudal fins. It is split vertically but unequally through the middle of the fish, so that the left side lies above the left of the head and the impression of the right squamation, and the impression of the right side of the head lies below.

*Shape and Size*.—The body was elongately fusiform, and the caudal body prolongation long and slender. The maximum depth is less than one-fifth the total length, and the head



TEXT-FIG. 4.—Head of *Fouldenia ottadinica*, gen. et sp. nov. The jaws are displaced downwards and forwards. [P. 13179.  $\times 4$ .]

Br. = Branchiostegal rays. Fr. = Frontal. Gr. = Grooves on mandible and maxillary border. I. temp. = Intertemporal. Md. = Mandible. Mx. ex. = Maxillary expansion. Mx. m. = Oral margin of maxilla. Op. = Operculum. Par. = Parietal. P. op. = Preoperculum. P. temp. = Post-temporal. S. temp. = Supratemporal. S. op. = Suboperculum. Tab. = Tabular.



TEXT-FIG. 5.—*Fouldenia ottadinica*, gen. et sp. nov. [P. 13180.  $\times 3\frac{1}{2}$ .]

Ros. = Rostral bones. S. cl. = Supracleithrum. "X." = Bone "X." Others as in text-fig. 4.

with opercular apparatus is approximately one-quarter (P. 13182–3). The orbit is large and placed far forward and low down.

Specimen P. 13182 (with counterpart P. 13183) measures 7.5 cm., but P. 13181 is the anterior part of a fish half as large again, and must have reached a total length of not less than 10 cm.

*Skull*.—Many of the features of the external skull and visceral bones are revealed in a number of specimens, but particularly well in P. 13179 (text-fig. 4), P. 13180 (text-fig. 5), and P. 13178 (text-fig. 6). A partial restoration is attempted in text-fig. 7.

(Cranium.)—The parietal is rectangular and longer than broad. To the exterior lies the oblong supratemporal, of which the inner margin is comparatively straight where it is in contact with the parietal and the hinder part of the frontal. In front and to the outside it forms an oblique and rounded suture with the intertemporal (P. 13183), which is imperfect in all specimens. The frontal is much longer than wide (text-fig. 6), but its precise limits are rather obscure. The circum- and post-orbital series are in no case preserved except for

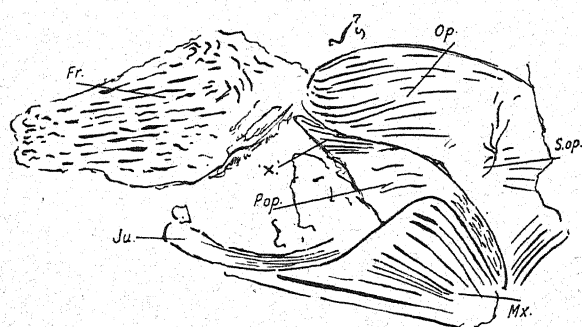
the jugal (text-fig. 6). Its limits are uncertain and it probably represents more than the one element. The bones of the snout are represented by the deeply grooved but obscure elements seen in text-fig. 5. The presence of a tabular row is proved by an impression of their ornament in P. 13179 (text-fig. 4).

(Visceral Skeleton.)—These bones are known for the most part by external impressions only. The suspensorium, though nowhere visible, must have been oblique, to judge from the disposition of the opercular series, but the gape seems to have been limited.

The mouth was rather small, for the jaw-bones are shorter than is usually the case and very obliquely placed, reminding one of the jaws of another Lower Carboniferous genus, *Canobius*.

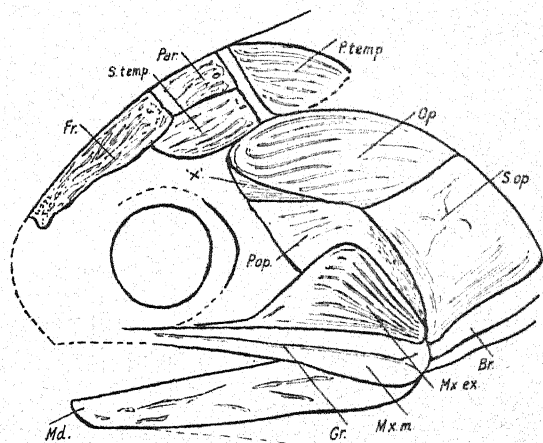
The maxilla has the form common to all palæoniscids, a narrow suborbital bar and a large posterior expansion; but the latter is remarkable in that it is shaped like an isosceles triangle with the apex rounded off. The mandible is short and stout with a straight upper, and a gently convex lower, border.

On account of the peculiar shape of the maxillary expansion, the form of the preoperculum



TEXT-FIG. 6.—*Fouldenia ottadinica*, gen. et sp. nov. Skull-roof and part of visceral skeleton. [Holotype, P. 13178.  $\times 4$ .]

Ju. = Jugal. Other lettering as in text-figs. 4 and 5.



TEXT-FIG. 7.—*Fouldenia ottadinica*, gen. et sp. nov. Partial restoration of head. The intertemporal, rostral, and circum-orbital series of bones are omitted. Lettering as before.

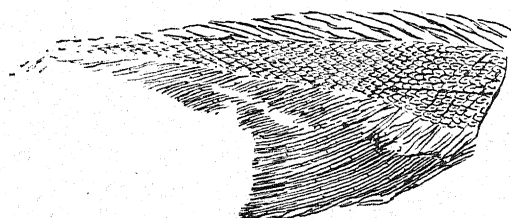
has been modified in an unusual manner. It is bent about its middle and expanded anteriorly as in most palæoniscids, but the upper limb is deeper than long and bent at right-angles to the lower. The long, straight anterior border is, of course, in contact with the postorbital series, and the upper with the wedge-shaped bone "X" (text-fig. 6). In P. 13179 the preoperculum is separated from the maxilla by the displacement of the jaw-bones forwards and down (text-fig. 4). The operculum is short and broad, with the upper and hinder margins confluent and rounded: it is oblique in position. The suboperculum is rather larger than the operculum and roughly square in shape. The dorsal and anterior margins are concave, the posterior convex and the lower front angle is produced. The branchiostegal rays are, with the exception of the first two or three immediately succeeding the suboperculum, obscured in every case, and their number is consequently unknown.

The ornament of the external bones of the head is for the most part rugose. On the skull-roof the rugæ are coarse and roughly longitudinal in direction, but irregular in places and frequently interrupted. On the jugal they are also numerous but very much finer, while on the expansions of the maxilla and preoperculum and the other opercular bones the rugæ are coarse and less crowded and vary in direction. On the operculum, bone "X," and maxillary expansion they are diagonal or roughly parallel to the sloping hinder and upper margins;



on the suboperculum they are irregularly radiating in the centre, but parallel to the periphery near the margin. But the most striking feature of the ornament is that on the oral margin of the maxilla and the lower jaw. These areas are quite smooth, but are deeply incised by grooves. In the case of the maxillary margin there is a single longitudinal groove bifurcated at the proximal end, but on the mandible the grooves are irregular and inconstant in form and direction (text-figs. 4, 5, 6). A similar ornament is present on part, at least, of the rostral bones.

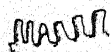
Dentition.—Teeth are for the most part missing; in one specimen only, P. 13183, are any visible. These, a series of six lying above the hinder end of the mandible, are small and peg-like. The crown is slightly expanded towards the top which is flattened. From their position and orientation they appear to belong to an inner row of the lower jaw (text-fig. 9).



TEXT-FIG. 8.—*Fouldenia ottadinica*, gen. et sp. nov. Almost complete tail, only the tip of the upper lobe being lost. [P. 13185.  $\times 2$ .]

Unpaired Fins.—The dorsal fin is well developed and the base long. The origin is far forward, opposite, if not anterior to, the insertion of the ventral fins (P. 13180), and the fin extends to a point opposite the middle of the somewhat smaller anal fin. In P. 13183, a speci-

men 7.5 cm. in length, the base of the dorsal fin is 1.5 cm. long, or about equal to the distance from its origin to the opercular opening, and equal to the maximum depth of the body. The number of rays exceeds thirty, but cannot be determined with accuracy; the rays increase gradually in length from the front to a maximum somewhat behind the middle of the fin, and the posterior border is somewhat excavated. The fin is therefore triangular, but the front slopes more than is usual in palæoniscids, and rather resembles in this respect that of *Holurus*, but it is taller, the longest ray being little shorter than the length of the base (TRAQUAIR, 1912, p. 169). The fin-rays are moderately broad and articulated throughout, while those that form the posterior edge are distally dichotomized. Large fulcra, described below, are present



TEXT-FIG. 9.—Posterior lower teeth. [P. 13183.  $\times 9$ .]



TEXT-FIG. 10.—Fulcral rays of lower caudal lobe. [P. 13183.  $\times 5$ .]



TEXT-FIG. 11.—Paired fulcral rays of lower caudal lobe. [P. 13182-3.  $\times 5$ .]



TEXT-FIG. 12.—Ridge-scale in front of dorsal fin. [P. 13178.  $\times 5$ .]

along the anterior margin. The anal fin is similar to the dorsal, but has a somewhat smaller base, and the number of fin-rays is accordingly less. The caudal fin is almost complete in P. 13185 (text-fig. 8). The body-prolongation is long and attenuated, but the only sign of the bifurcation of the fin, which is deep, is a gentle excavation of the hinder margin. The anterior rays of the lower lobe are more steeply graduated than in the other median fins, but in all other characters they are identical.

The so-called fulcra, which form such a conspicuous feature of the fins of this fish, are interesting in that they appear to be nothing more than the expanded ends of the anterior rays (text-fig. 10). Unlike the fulcra of most palæoniscids, they are not attached to other



rays and have retained their connection with the base. Anteriorly, where they are stouter, they are certainly paired; these large fulcral rays are commonly found detached when the fin has been disturbed in fossilization, and render the identification of this form easy. They grade quite imperceptibly into the median ridge-scales: it is quite impossible to decide where the one ends and the other commences (text-fig. 11).

**Paired Fins.**—The shape of the pectoral fin is not known, for only the basal portion, mostly as impressions (P. 13178, P. 13182-3), and a few scattered rays (P. 13180) are preserved. It had a large, curved base comprising at least thirty lepidotrichs, which seem to have been similar in size to those of the median fins, and with the same fulcral expansions forming the cut-water; the extent of articulation and dichotomy, if any, is not shown.

The basal stumps of the ventral fin-rays are all that are preserved of these fins, but they serve to fix their position, *i.e.* opposite or slightly behind the origin of the dorsal fin (P. 13180).

**Squamation.**—The squamation is in every respect normal. The body is covered by scales of the usual rhomboid form, which are deepest on the anterior part of the flank and diminish in height in all directions, becoming very shallow ventrally. There are also the typical reversed rows of small, diamond-shaped scales on the caudal body prolongation. The number of vertical rows of body-scales as far as the origin of the lower caudal lobe is approximately fifty, and the 9th row from the operculum contains twenty-six or twenty-seven scales (P. 13180).

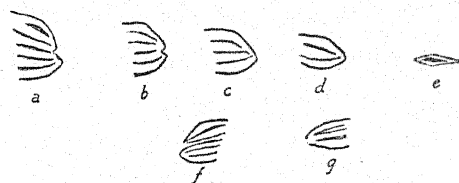
The flank-scales, of which the largest are somewhat taller than broad, are moderately thick, and bear a conspicuous vertical rib on the inner surface, but a peg-and-socket articulation seems to be absent. The area of overlap amounted to one-quarter of the total breadth in some cases.

There is a series of large V-shaped ridge-scales extending from the occiput to the dorsal fin and from behind the latter backwards along the upper margin of the tail. A ventral series runs from behind the anal fin to the lower caudal lobe. These ridge-scales vary in shape quite normally; the most anterior are oval, and these become more and more elongated towards the rear until they grade into the fulcral rays of the fins (text-figs. 11, 12).

The ornament on the body-scales is very distinctive. It consists chiefly of a few coarse, roughly horizontal rugæ, which tend to converge at the middle point of the hinder border. The uppermost ruga is generally turned down somewhat in the deepest scales, but in the shallower forms, where there are fewer rugæ, this uppermost ridge bends down to meet the lowest member, which is somewhat turned up, and so forms the hinder margin (text-fig. 13). Posteriorly the ridges are much reduced in number, and the scales on the tail have only two, divided by a median groove, while those on the body prolongation are ornamented with a median pit only. The ridge-scales are decorated with a few coarse, horizontal ridges.

**Lateral Line.**—A few scales of the lateral line are preserved in P. 13178, P. 13180. They show that the lateral line opened on to the surface by a posterior notch.

**Remarks.**—This little fish shows a number of striking peculiarities which make it unlikely to be confused with any other form. The large suboperculum and the triangular maxillary expansion are also found in *Canobius* (*C. ramsayi*, TRAQUAIR, 1912, p. 172), but the form and obliquity of the preoperculum and the ornament of the maxilla and mandible are utterly different. The shape of the median fins is to some extent reminiscent of *Holurus*, but the peculiarities are not so exaggerated. To no other palæoniscid does it bear any particular



TEXT-FIG. 13.—*Fouldenia ottadinica*, gen. et sp. nov. (a-c), flank scales; (d), caudal; (e), scale of body prolongation; (f) inferior flank; (g) anterior ventral scales. [a-d, P. 13178; e, P. 13182; f-g, P. 13180.  $\times 7$ .]

likeness, and the condition of the fulcral rays, which for reasons discussed later may be considered primitive, tends further to isolate this form.

Genus CARBOVELES,\* nov.

Trunk tapering from pectoral girdle, rather stout; head large with blunt snout. Mandibular suspensorium oblique, gape wide; mandible very stout; teeth of upper jaw small and sharply conical, flanked by an outer row of minute denticles; lower teeth similar with smaller row on inside. Fins with numerous delicate rays, articulated throughout; fulcra unknown. Dorsal and anal fins long-based and placed far back, the former arising a little in front of latter, which is almost continuous with lower caudal lobe. Anterior rays of anal (and dorsal) short, increasing to a maximum length behind. Caudal body prolongation slender, lobes well developed. Trunk covered with small, thin, rounded scales rarely preserved; normal squamation only on most posterior part of caudal body prolongation.

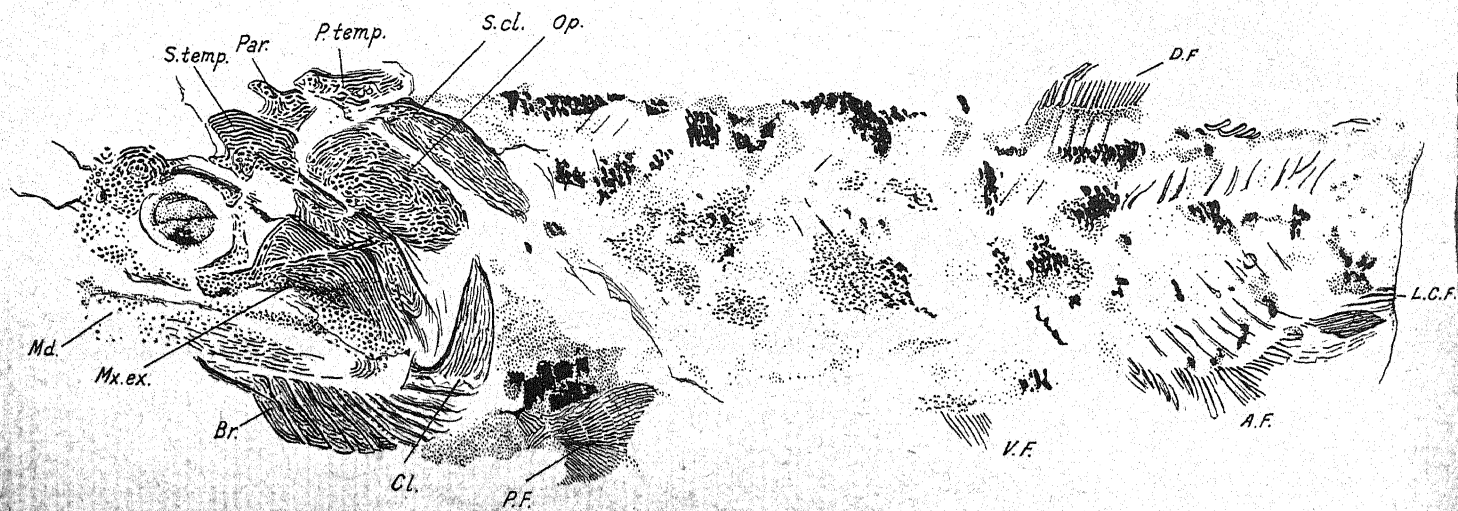
*Carboveles ovensi*, sp. nov.

(Text-figs. 14-17.)

*Holotype*.—Imperfect fish, Brit. Mus., P. 13120.

*Paratypes*.—Two specimens, Brit. Mus., P. 13121 and P. 13184.

*Description of Specimens*.—The holotype shows the head excellently in impression, the form of the body and portions of all the fins except the caudal, of which only the most anterior



TEXT-FIG. 14.—*Carboveles ovensi*, gen. et sp. nov. Holotype. [P. 13120.  $\times 2$ .]

Cl.=Cleithrum. P.F., D.F., V.F., A.F.=Pectoral, dorsal, ventral, and anal fins. L.C.F.=Anterior scales of lower caudal lobe. Other lettering as before.

of the lower ridge-scales are left. The pectoral fins are imperfect distally, and only a few rays of the ventral and the proximal portions of the dorsal and anal fins are present. P. 13121 is a caudal region which shows almost the whole of the median fins; only the tip of the upper caudal lobe is missing. P. 13184 is an imperfect head in which part of the crushed palate is exposed from the aboral aspect.

*Shape and Size*.—The head is very large in comparison with the body and has a blunt

\* Lat. *Carbo*=coal; *Vales*=a light-armed warrior.



snout. The contour of the back is almost straight, and that of the lower surface is but slightly curved until the anal fin is reached; the body is therefore almost wedge-shaped. The caudal body prolongation is narrow and rather long.

The largest specimen, the holotype, measures 7.5 cm. from snout to lower caudal lobe, and has a maximum depth of 2.8 cm.

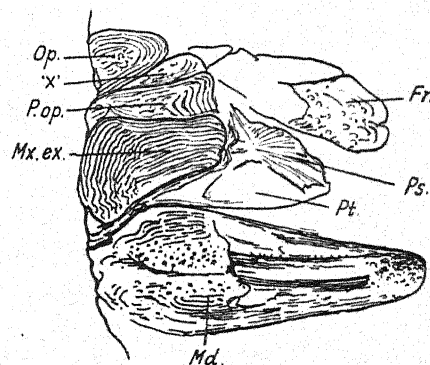
Skull—(Cranium).—The base of the cranium is protected by a broad parasphenoid, imperfectly shown in P. 13184 (text-fig. 15). The aboral surface is completely convex, but, except for the pituitary depression and the centre of ossification at the base of the ascending processes, no features are observable, and the associated palatopterygoid is too much crushed to show any details. The external bones are observable in the type-head in impression and in P. 13184, which shows the impression of the left side of the head and the actual bones of the right side (text-fig. 15). The parietal is somewhat irregular in shape. The hinder and outer margins are straight, but the inner is irregular and longer than the other three, as the bone is produced forwards along the median line, and the anterior margin is correspondingly sigmoidal. This bone and the supratemporal are somewhat out of place in P. 13120 (text-fig. 14), the hinder margin being almost at right angles to its natural position. The supratemporal is not unlike the smaller parietal in shape. The inner side of the anterior margin is produced forwards in a similar manner, but the inner suture is more regularly convex and the outer seems less regular although it is not clearly shown. The frontals, intertemporals, and tabulæ are obscure or missing entirely, and the details of the bones on the snout are lost. The large orbit is surrounded by the usual series of circum-orbitals, but here again precise information as to shape is wanting.

The ornament of the skull-roof consists chiefly of rugæ in varying degrees of interruption. Those on the supratemporal are for the most part whole, except along the outer border, and run regularly parallel to the parieto-frontal margin. The rugæ on the other skull-bones are quite irregular, with an occasional tendency to form parallel series, and are much broken up especially on the snout, which is largely tuberculated.

(Visceral Skeleton).—As mentioned above the palate is too fragmentary for description. The suspensorium, seen in impression on the preoperculum (text-fig. 14), was very obliquely placed and the mouth very long, so that the gape must have been considerable. The maxilla has the normal shape with a very large maxillary expansion, of which the upper margin is indented and the hinder slopes to the rear, while the oral border is turned downwards conspicuously in the posterior half. The premaxilla is wanting, but the dentary is seen to be deep and long.

The preoperculum is narrow in both the horizontal and vertical portions and the former is particularly long. Above it lies the wedge-shaped bone "X." The operculum is large and oblique in position. It has acute antero-superior and postero-inferior angles, while the upper supplementary angle is rounded. The suboperculum is absent in both specimens, but the impression of about fourteen broad branchiostegal rays are preserved in the type; their average breadth is about 1.5 mm. and their length 5 mm.

The ornament of the visceral bones is similar to that of the cranial elements. The rugæ



TEXT-FIG. 15.—*Carboveles ovensi*, gen. et sp. nov.  
Imperfect head, partly in impression.

Pt. = Palatopterygoid. Ps. = Parasphenoid.  
Other lettering as before. [P. 13184.  $\times 2$ .]

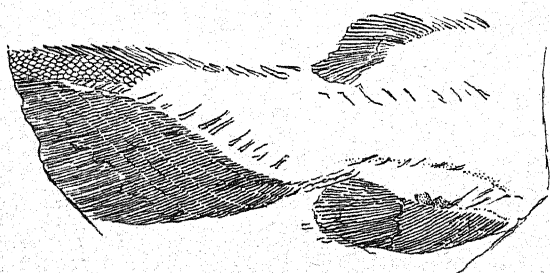


are uninterrupted on the maxillary expansion except along the oral border, which is strongly tuberculated; they run parallel with the upper and hinder margins. In the holotype (text-fig. 14) this ornament is disturbed by an oblique cut which continues on to the preoperculum. This is doubtless the result of an injury which must have been inflicted on the fish when quite young, for the rugæ are not abruptly cut, but have been adapted by curving round parallel to the scar. The suborbital bar is wholly tuberculated and a similar ornament covers all but the hinder ventral area of the dentary. The sculpture of the opercular bones and "X" is somewhat variable, for that in the holotype is far more broken up than that in P. 13184 (text-fig. 15). On the whole the rugæ run parallel with the periphery, and the branchiostegal rays are similarly decorated.

Dentition.—The dentition is rather feeble. It is seen in P. 13184 alone, and there only in part.

The principal row in both jaws is composed of relatively small, narrow, sharply pointed teeth, and outside these is a series of minute denticles which seem to grade into the tubercular ornament.

Internal to the principal row of the lower jaw is, in addition, a series of numerous similar but smaller teeth.



TEXT-FIG. 16.—*Carboveles oveni*, gen. et sp. nov.  
Posterior half of fish. [P. 13121. x2.]

Axial Skeleton.—Impressions of the neural and hæmal bones are preserved in both P. 13120 and P. 13121, but they are only doubtfully represented in the abdominal region (text-fig. 14). Caudally, the hæmal spines are expanded at the tip to support the lower lobe of the tail (text-fig. 16).

Unpaired Fins.—The fin-rays are slender and numerous. Each is ganoine-covered and articulated throughout its length, but, owing

to the imperfect state of the specimens, the dichotomy of the distal end can only be seen in the anal fin (P. 13121), though doubtless it was present in all fins.

The dorsal and anal fins are similar in form, although the first is somewhat the larger. The anterior rays are more slowly graduated than in most palæoniscids, and the maximum height is about the middle of the fin. In these respects the fins resemble those of the allied genus *Phanerosteon* (TRAQUAIR, 1912, p. 167). In neither fin in P. 13121 is the posterior border perfect. The number of rays is about 35 in the anal fin, but cannot be ascertained in the dorsal, as the anterior part is missing.

The radials of the dorsal are faintly indicated in the holotype, and those of the anal in both that specimen and P. 13121. There is only one series present in the anal fin. Both fins are placed very far back. The dorsal is somewhat anterior to the anal, which is almost continuous with the lower caudal lobe.

The rays of the tail are similar to those of the other fins. The proximal articula of the rays is double the length of the more distal, and is not covered with ganoine in the near half, where it is actually covered by the pedicle.

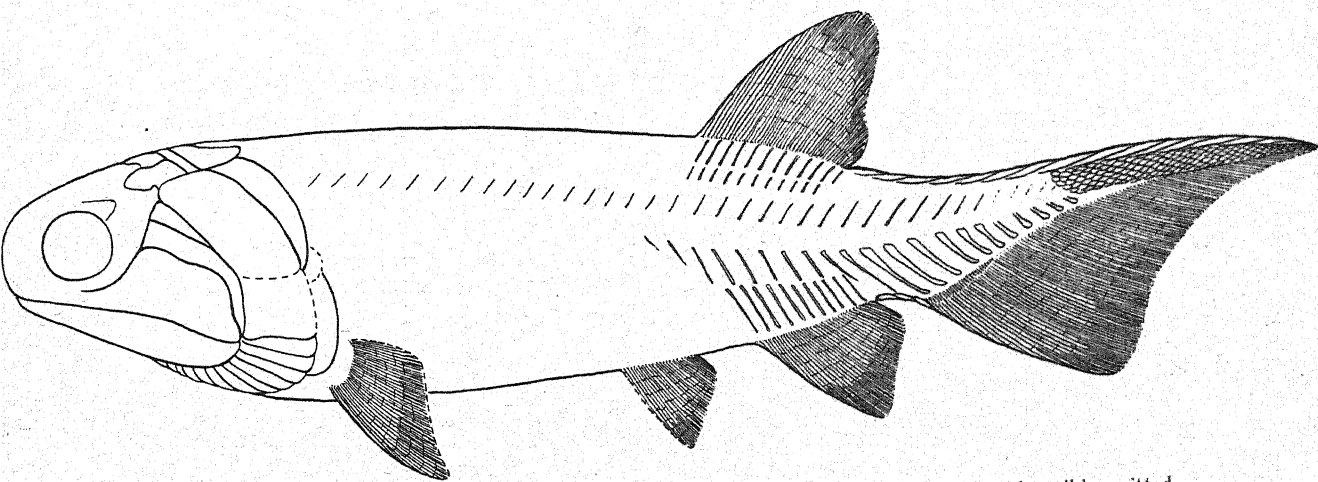
The shape of the fin is doubtful, as it is not wholly preserved, but the rays are all very long except where they are graduated in front as in the other median fins, and it is most likely that it was less forked than usual; or, if it were forked, the lobes must have been exceptionally long.

It is only in front of this fin that the anterior ridge-scales can be seen grading into the frontmost rays, but there is no sign of fulera on this or any other fin.

Paired Fins.—The pectoral girdle is of no special interest. The post-temporal has the form of an isosceles triangle, of which the acute basal angles are truncated. The supra-cleithrum is elongated and the cleithrum broad. The impression of the latter obscures those of the suboperculum and posterior branchiostegal rays in the holotype.

The ornament of the post-temporal is irregular, like that of the parietal, while the supra-cleithrum and cleithrum are covered with broken rugæ which run roughly parallel to the length of the bones.

The proximal part of the left pectoral fin is well displayed in the holotype. It shows a remarkably large number of lepidotrichia which are articulated to the base. The proximal segment is double the length of the more distal segments, which become progressively stouter; consequently, it is almost certain that the rays dichotomized in the distal parts not now preserved. Nineteen rays are actually present and there are the impressions of 23 more, making a total of at least 42 lepidotrichia; the base is in consequence very long and curved. In front of the fin-rays proper there are about 8 of the usual ray-like ridge-scales. They are short in front, but gradually increase in length and become more slender and ray-like until they grade



TEXT-FIG. 17.—Restoration of *Carboveles ovensi*, gen. et sp. nov. The squamation except on the tail is omitted.  
[About  $1\frac{1}{2}$   $\times$  nat. size.]

into the lepidotrichia of the fin. In front they are crushed, and the two halves are somewhat separated. There are no fulcra.

The position of the ventral fins, opposite a point immediately in front of the dorsal fin, is indicated by the basal segments of the fin-rays. Nothing else is preserved.

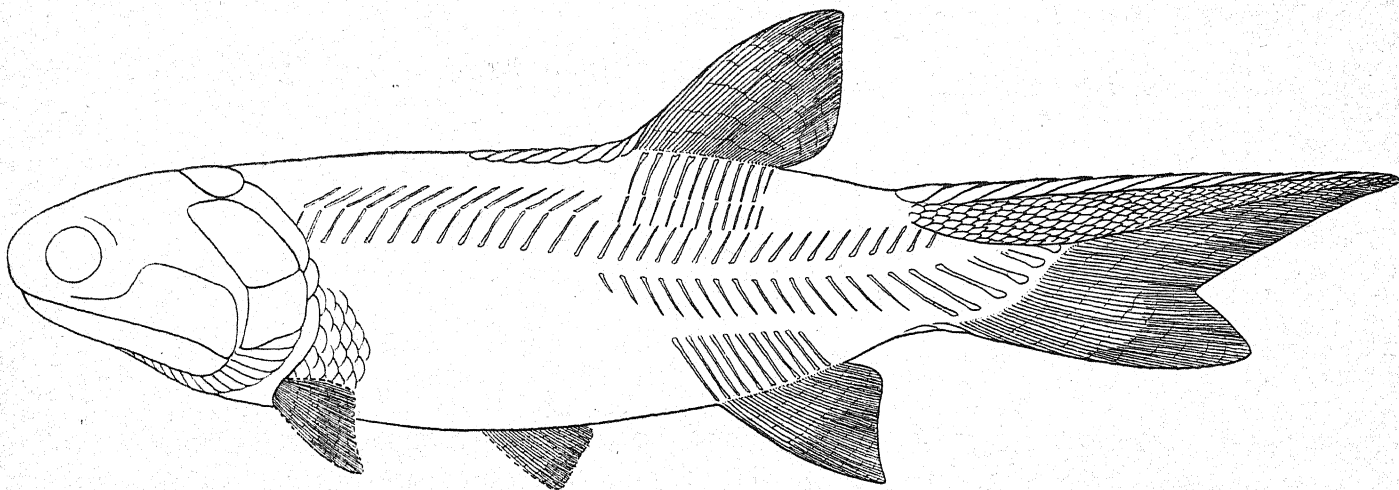
Squamation.—The extent of the squamation is not at first obvious, but it becomes clear from the scattered fragments that are distributed irregularly over the body of the type-specimen that the whole was covered with delicate scales which have been only partially preserved. As in most palæoniscids with degenerate squamation these thin scales are cycloid and deeply overlapping. The posterior part of the caudal body prolongation is covered with normal scales oval in shape, which are ornamented with concentric rugæ, and start quite abruptly.

The usual series of fulcral ridge-scales protects the upper border of the tail. They are numerous, thin, and long, and even in front do not show the broad oval form with which the series usually commences.

Remarks.—This fish has obvious affinities with TRAQUAIR'S genus *Phanerosteon*, for there are a number of features in common. Both have similarly shaped bodies with large



heads, while the internal skeletons were undoubtedly similar,\* as far as can be judged, and the dorsal and anal fins are identical. In the tails, however, differences of importance occur; for there can be little doubt that the lobes in *Carboveles* were less forked than in *Phanerosteon*, although the actual shape of the tail in the former is uncertain. The paired fins in either case



TEXT-FIG. 18.—Restoration of *Phanerosteon mirabile* Traquair. [Modified after Traquair. About  $1\frac{1}{2} \times$  nat. size.]

are imperfectly known. It is in the squamation that the distinction is most apparent, and the very differences only serve to bring out their close relationship, for they are differences of degree only. In *Carboveles* the squamation is thin and on the point of disappearing, except along the caudal body prolongation, which is covered by the usual reversed series;



TEXT-FIG. 19.—*Phanerosteon mirabile* Traquair. Posterior half of well-preserved fish. [P. 11665.  $\times 2$ .] A. Anal radials showing osteomes. [ $\times 4$ .]

in *Phanerosteon* the squamation has completely disappeared save in those areas in which it is strongest in *Carboveles*, although the extent of the small caudal scales is much greater in this than in the new genus.

#### Genus *ÆTHERETMON*,† nov.

Trunk fusiform; head rather big with blunt snout and large orbit anteriorly placed. Mandibular suspensorium oblique and gape wide. Teeth in two series, those of the outer

\* The internal skeleton of *Phanerosteon* has not been well-figured, and the caudal region in TRAQUAIR'S restoration is obviously faulty. A new restoration is given here, based largely on P. 11665 (text-fig. 19) which is beautifully preserved. This specimen is of further interest as it shows on the anal radials "bladder-wrack" osteomæ, which are so common in some types of living fish. This must be the earliest pathological record (see R. L. MOODY, 1923, chap. iii).

† *αἴθερς* = strange; *ἑρμῶν* = a paddle.



being small, conical, and clustered, variable in size; inner teeth larger, stoutly conical, and incurved, well and evenly spaced. A series of at least 5 postorbitals. Operculum oblique, twice as deep as broad; suboperculum large and rectangular; branchiostegal rays slender and numerous. External bones of head and opercular apparatus with rugæ, often interrupted and becoming tuberculate in front; pectoral arch longitudinally striated. Post-cleithrum and clavicle large. Fins well developed with a few very long fulcra partly interstitial between the graduated anterior rays. Fin-rays covered with ganoine, dichotomizing distally, those of pectoral fin inarticulate; remainder articulated throughout. Pectoral fin paddle-shaped; dorsal and anal fins long-based, triangular; origin of dorsal somewhat anterior to that of anal. Caudal fin deep and very inequilateral, but not strongly forked; lower lobe somewhat rounded. Squamation regular; scales ganoid, thick, with conspicuous overlap; series of enlarged azygous ridge-scales along dorsal and ventral borders; paired posterior anal scales greatly enlarged.

This genus contains one species, the genotype:—

*Ætheretmon valenticum*,\* sp. nov.

(Text-figs. 20–38.)

*Holotype*.—Imperfect fish, Brit. Mus., P. 13145 (with counterpart, P. 13146).

*Paratypes*.—Thirty-one specimens, seven in counterpart, Brit. Mus., P. 13147–P. 13177, P. 13189–P. 13190.

*Description of Varieties*.—There are two distinct varieties of this fish. These were at first considered to be distinct species, but on the accession of new material, intermediate forms were discovered, and in spite of the striking differences of the extreme types, the idea of their specific distinctiveness had to be abandoned in favour of that of a single species, which, like *Elonichthys robisoni* (TRAQUAIR, 1901, p. 62), was very variable in certain subsidiary features.

All the specimens of the *forma typica* are smaller than the holotype of the variety, but the differences between the two cannot be due to age, for the intermediate forms are generally of the same size as, if not smaller than, the largest typical specimens; it may be that the variety attains a somewhat larger size than the ordinary form, but on the other hand the disparity in size may be entirely fortuitous.

The differences between the two forms lie otherwise entirely in the superficial ornament of the external bones and the scales, and as the holotype of the variety demonstrates certain anatomical features more plainly than the other specimens, the whole of the material will be described together.

*Diagnoses of Varieties*:—

A. *Ætheretmon valenticum*, *forma typica*.

Length not known to exceed 7.5 cm. Mandible ornamented with two series of rugæ meeting at a very acute angle, the lower rugæ being very long and nearly parallel with the lower jaw margin. Rugæ on maxillary expansion, operculum and suboperculum whole and well separated, relatively few in number. Ornament of anterior expansion of preoperculum composed of rugæ roughly parallel with margins of bone. Anterior flank-scales with lower margin only very slightly convex and lower horizontal rugæ scarcely curved and not coalescing posteriorly.

\* *Valentia* was the Roman Province in which the Foulden area was situated.

B. *Ætheretmon valenticum* var. *ovensii*, nov.

A variety attaining a length of 9.0 cm. Rugæ of mandibular ornament short and meeting at a large angle; rugæ on maxillary expansion, operculum and suboperculum numerous and close and, on the last two bones, frequently interrupted. Ornament of anterior expansion of preoperculum composed of much interrupted vertical ridges, becoming tuberculate behind. Anterior flank-scales with very convex inferior margin and lower ornamental ridges correspondingly curved and coalescing to form lobes at posterior border.

• *Holotype of Variety*.—Brit. Mus., P. 13175 (with counterpart, P. 13176).

*Paratype*.—Brit. Mus., P. 13177.

*Description of Specimens*.—The specific holotype, P. 13145-6, shows all the principal features noted above except the distal portions of the median fins. The holotype of the

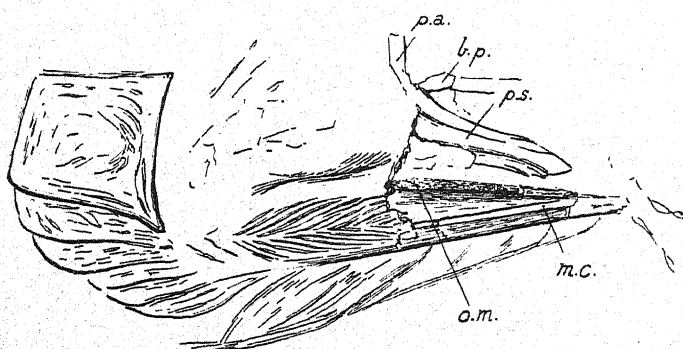
variety is also very well preserved and the features of the facial bones are especially well shown, but the skull-roof and the fins are for the most part missing. All the specimens are imperfect, but collectively demonstrate nearly all the characters of the external anatomy in the adult and the young.

*Shape and Size*.—The fish is typically fusiform in outline with a large head, blunt snout, and well-developed fins.

Its size is small; the largest specimen, the varietal holotype, is 9.0 cm. long, and has a maximum depth of 2.4 cm.; while the *forma typica* attains a maximum length of about 7.5 cm. and a depth of 2.0 cm. (P. 13145).

• *Skull*—(Cranium).—The oral face of the parasphenoid (text-fig. 20) is strongly convex but flattened out along the lateral borders, forming a prominent central ridge. Of the two lateral processes the hinder undoubtedly belongs to the parasphenoid and is the ascending process, while the anterior seems to be a remnant of the basipterygoid process and is the only portion of substitution bone left.

The bones of the snout are not preserved in any specimen, and the frontals are always fragmentary. The parietals (text-fig. 21) are small and rectangular, but the flanking supratemporal is more irregular in form. Its inner, hinder, and outer margins are roughly straight, and of these the inner is the longest. The anterior margin is in contact with both the frontal and the intertemporal, and somewhat produced forward between the two, so that it is doubly concave with the intertemporal contact much the longer. The intertemporal is also irregular in form as far as this is known: the posterior margin where it is in contact with the supratemporal is, of course, convex; and the outer, which is bounded by the postorbitals, preoperculum, and "X," is almost straight. The form of the anterior margin is unknown and the frontal is in no case preserved. A tabular row was certainly present, but only one element can be seen distinctly. The postorbitals (text-figs. 21, 22) are at least five in number and occur in three rows, of which the most anterior contains only one bone. This forms the posterior boundary to the orbit, and is almost vertical, with a more or less straight orbital border and

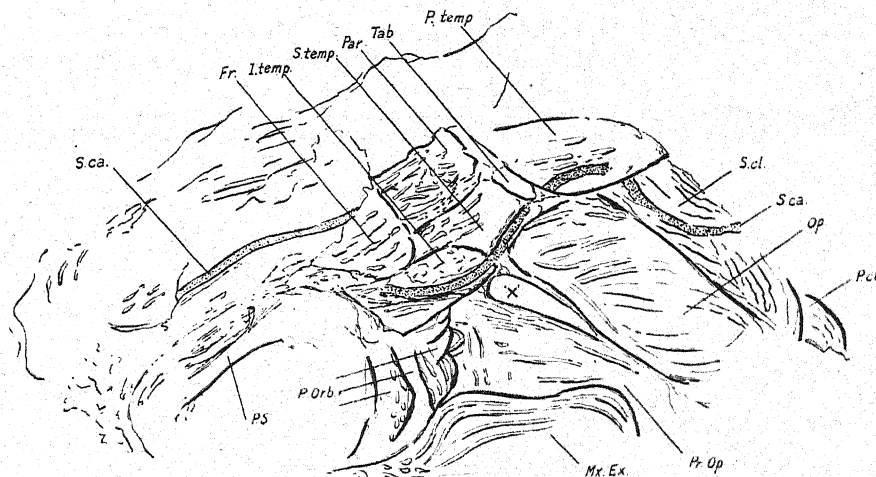


TEXT-FIG. 20.—*Ætheretmon valenticum*, gen. et sp. nov. Visceral skeleton. [P. 13166.  $\times 4\frac{1}{2}$ .]

b.p. = Basipterygoid process. m.c. = Mandibular canal. o.m. = Oral margin.  
p.a. = Processus ascendens. p.s. = Parasphenoid.



an obtusely angulated hinder margin. Behind this is another elongated, vertical bone, shaped like a boomerang. The upper half is in contact behind with the posterior row of postorbitals which are quite small and at least three in number; there may be a fourth, for the arrangement of the series in contact with the suborbital bar of the maxilla cannot be seen. The shape of



TEXT-FIG. 21.—*Etheretmon valenticum*, gen. et sp. nov. Crushed head from left side, showing details of bones and sensory canals. [P. 13154.  $\times 4\frac{1}{2}$ .]

P. cl. = Postcleithral scale. P. Orb. = Postorbitals. S. ca. = Sensory canal. Other lettering as before.

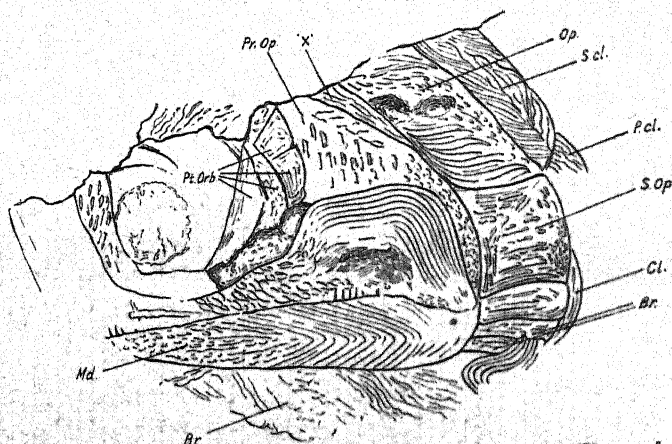
these small four-sided plates is variable; for the upper two are broader than deep while the lowest is deeper than broad. In each the front margin is gently concave and the posterior convex.

The sculpture of the bones of the roof of the skull and snout is composed of well-defined rugæ, which coalesce in series of six or seven and are interrupted to a varying extent in different individuals; in the holotype (P. 13145-6), and in P. 13156 they are quite uninterrupted, but in the majority of specimens they are broken up into various lengths. The general direction of this ornament is longitudinal.

The two large, anterior postorbitals are tuberculated, but the smaller bones are decorated with concentric ridges.

(Visceral Skeleton.)—The inner arcade is present in many specimens, but in a fragmentary state, and no details are available.

The suspensorium is itself unknown, but, to judge from the disposition of the opercular bones, it must have been very obliquely placed and the gape correspondingly wide. The maxilla is of the usual palæoniscid form. The expansion is trapezoidal in shape and nearly twice as long as deep. The upper border is gently indented, and the oral margin curved downwards behind. The mandible is long and moderately stout; the upper margin is straight and the lower curved. This bone is, as usual, deepest behind. In P. 13172 a complete dentary,



TEXT-FIG. 22.—*Etheretmon valenticum*, var. *oveni*, nov. Figure of head of P. 13175-6.  $\times 4$ . Lettering as before.



probably belonging to this species, is exposed from the inside, and a cast of the same surface is preserved in the counterpart. In both specimens the articular end and the covering pre-articular bone are missing. The course of the mandibular canal can be traced with ease, running at first near to, and parallel with, the inferior border, and then rising in front and continuing beneath the dentigerous flanges of the dentary.

The preoperculum is normal in shape. It is sharply bent about the middle, and the anterior border is as deep as the expansion is long (text-fig. 22: in text-figs 21 and 24 it seems shallower owing to crushing). Between this bone and the operculum lies the narrower, wedge-shaped bone "X." The operculum is rhomboidal and oblique, with the obtuse angles rounded off, and is twice as high as broad.



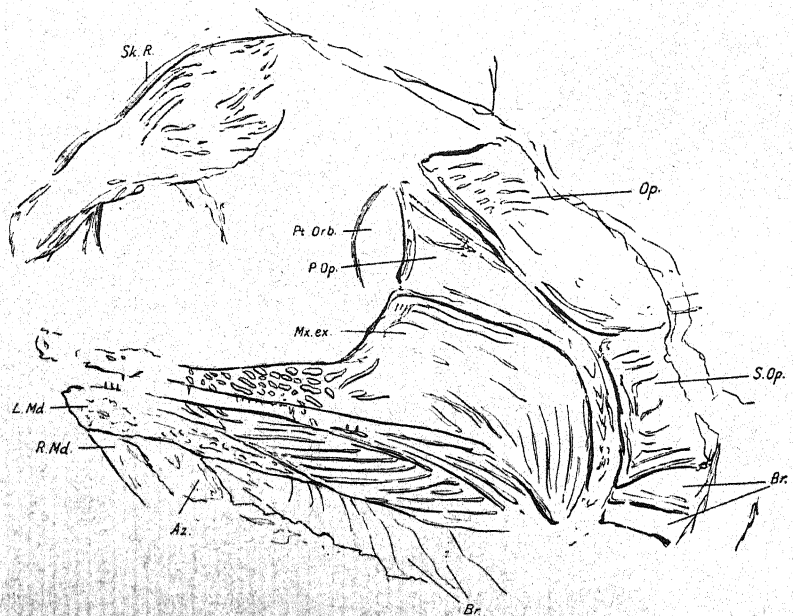
TEXT-FIG. 23.—Internal impression of right mandibular ramus of ? *Etheretmon valenticum*, gen. et sp. nov. [P. 13174.  $\times 3\frac{1}{2}$ .]

The suboperculum is nearly square; all margins but the hinder are slightly concave, and the two anterior angles are somewhat produced. The branchiostegal rays are slender; the first two immediately succeeding the suboperculum are broader than the others, and those under the angle of the jaw are the longest. Their number cannot be ascertained as the margins are obscured by the ornament. In one specimen there seems to be an anterior azygous plate (text-fig. 24, *Az.*).

The ornament of the visceral bones is partly rugose and partly tuberculate. On the suborbital bar of the maxilla large pyriform tubercles predominate, but the posterior expansion is covered with rugæ running roughly parallel with the periphery; these are closer and more numerous in the variety *ovensis* than in the typical form.

It is in the sculpture of the dentary and preoperculum that the two forms differ most. The ornament of the dentary is composed of two series of oblique rugæ which cut the upper and lower margins of the jaw and meet to form a series of backwardly directed angles. In the typical examples, e.g. the holotype, the lower rugæ are very nearly

parallel with the ventral margin of the jaw, and the upper series are scarcely more oblique, so that the angle formed by their junction is very small (text-fig. 25). On the other hand, in the varietal holotype (text-fig. 22), both series are quite oblique and form a bold herring-bone pattern. Intermediate stages are shown by other specimens. In all cases the rugæ become less regular and more longitudinal in direction towards the front and pass into a tubercular ornament under the snout. The sculpture of the anterior expansion of the preoperculum consists of rugæ concentric with the periphery; in the variety the whole is covered with

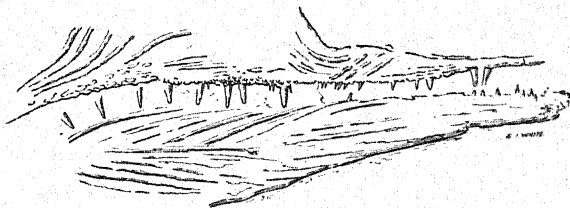


TEXT-FIG. 24.—*Etheretmon valenticum*, gen. et sp. nov. [P. 13147.  $\times 4\frac{1}{2}$ .]

*Az.* = ? Azygous plate. *L.Md.*, *R.Md.* = Left and right mandibular rami.  
*Sk.R.* = Skull roof. Other lettering as before.

vertical rows of tubercles. In both cases the lower limb is tuberculated, and the ornament of the other visceral bones is the same in all specimens, except that the rugæ, as on the maxillary expansion, are closer and more numerous in the variety than in the typical form. The rugæ on the operculum are roughly diagonal, but at the border they run parallel to the length of the bone. A similar type of ornament, but less regular in the centre of the bone, is present on the suboperculum. Both bone "X" and the branchiostegal rays are longitudinally ridged.

Dentition.—The teeth of the maxilla and lower jaw appear to be similar in size and arrangement. Along the oral border there is a series of numerous, small, pointed teeth. They vary irregularly in size between minute denticles, which seem to grade imperceptibly into the tubercles of the jaw ornament, and sharply pointed teeth about half as large as the inner row of laniaries (text-fig. 25). Their grouping is entirely irregular. The laniaries are



TEXT-FIG. 25.—Jaws and dentition of *Etheretmon valenticum*, gen. et sp. nov. [P. 13151.  $\times 4\frac{1}{2}$ .]

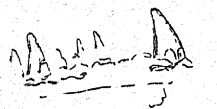
stoutly built for their size and sharply pointed (text-figs. 23, 25, 26). The tips are incurved and their spacing and size nearly constant, except that in front of the mandible they become smaller and are more crowded. At least eleven are seen in the maxilla of P. 13151 (text-fig. 25) and about sixteen on the lower jaw of P. 13174 (text-fig. 23) and its counterpart P. 13172. The latter are firmly fixed on to a horizontal flange of the dentary. No other teeth are preserved.

Axial Skeleton.—Nothing of this is to be seen.

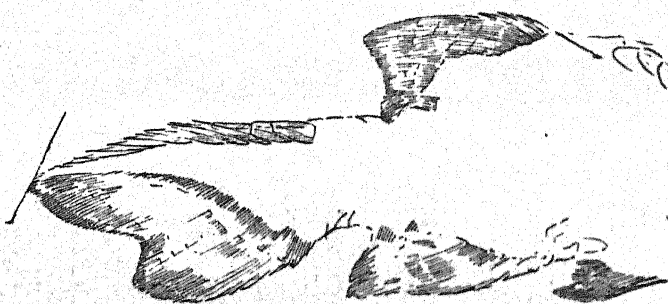
Unpaired Fins.—The dorsal and anal fins are both of the same shape and about equal in size. They are largely opposed, but the origin of the former is slightly anterior to that of the lower fin. The shape is broadly

triangular, with a blunted apex and an excavated posterior border. The number of rays, which are very fine, is large, approximately fifty in each fin (Dorsal: P. 13150, P. 13161. Anal: P. 13175, P. 13167). The anterior fin-rays are graduated in length, and the tips of the rays in front of the apex of the fin are expanded and covered with ganoine; it is difficult to detect the presence of the long fulcra interpolated between the free-ends of the rays. These fulcra are found on all the fins and are very characteristic of the fish. They will be described more fully with the pectoral fins. The fin-rays are covered with ganoine and articulated rather distantly at the base, but more closely towards the tips, where they dichotomize once.

The most perfect caudal fin is shown in P. 13161 (text-fig. 27), and of this only the extreme tips of the lobes are missing. The fin is deep and powerful and, although strongly inequilateral, it is only moderately cleft and the lobes are rounded. The fin-rays are precisely similar to those described above; they number approximately one hundred in the two lobes.



TEXT-FIG. 26.—*Etheretmon valenticum*, gen. et sp. nov. Portion of lower jaw with two laniaries and impressions of smaller outer series. [P. 13172.  $\times 7$ .]



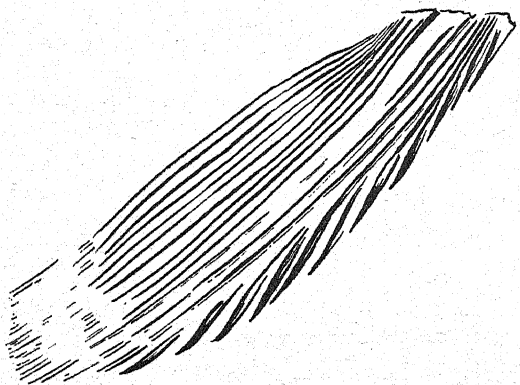
TEXT-FIG. 27.—*Etheretmon valenticum*, gen. et sp. nov. Hinder half of small fish showing median and ventral fins. [P. 13161.  $\times 2$ .]



**Paired Fins.**—The shoulder-girdle presents no features of particular interest—post-temporal, supracleithrum, cleithrum, clavicle, and postcleithral scale are all well-developed. They are ornamented with rugæ which on the supracleithrum have a tendency to form a herring-bone pattern.

Each of the paired fins is shown in at least two specimens, and they present features of considerable diagnostic value.

The pectoral fin is well-preserved in the holotype, but it is imperfect distally; in P. 13148-9 it is complete (text-fig. 28). The shape



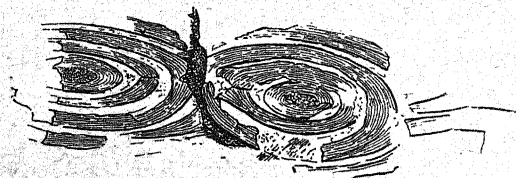
TEXT-FIG. 28.—*Etheretmon valenticum*, gen. et sp. nov.  
Pectoral fin showing arrangement of fulcræ. [P. 13148-9.  $\times 8$ .]

is lobate and elongated with the posterior rays, but little shorter than the longest. The length is 8.5 cm. in P. 13148-9 and about 10 cm. in the holotype. The number of rays is thirteen in each specimen, and they are unique in that they are unarticulated throughout their length; but as in most other palæoniscids the fin-rays dichotomize distally.

The peculiar fulcræ which characterize all the fins of this fish are particularly well-shown in the pectoral. The fin commences with one or two of the usual short anterior "ridge-scales," which are succeeded by a few graduated rays, and between these are interpolated a series of about ten very long fulcræ. The latter are like fin-rays which have lost their connection with the base and have become secondarily attached to the other graduated rays. Like the latter they have a long overlapped portion, and the uncovered distal part is somewhat expanded and covered with ganoiné. The majority of these fulcræ alternate with the tips of the fin-rays, but the most distal members of the series are all attached to the foremost long ray of the fin without any other rays intervening.

The origin of the ventral fin is considerably behind the mid-point between the pectorals and the anal. The ventral fin (P. 13161, P. 13148) is smaller than the pectoral, but it is well-developed and contains at least twenty rays (text-fig. 27) which are segmented throughout. The articulations of the rays are comparatively distant proximally, but increase in frequency towards the tip. The shape of the fin seems to have been triangular or rounded and the base relatively long, and the same series of elongated fulcræ borders the anterior margin as in the other fins.

**Squamation.**—The scales are brilliant and ganoid; those on the body are thick and rhomboidal in shape, with a strongly denticulated posterior margin. They undergo the normal variations in shape and size according to their position. There are five principal rows of flank-scales much deeper than wide, and of these the uppermost bears the lateral line. The depth of the scales decreases dorsally, ventrally, and to the rear, and they are especially shallow on the belly and back. There are the usual reversed rows of small lozenge-shaped scales on the caudal body prolongation. A strong peg-and-socket articulation is plainly visible in the very worn scales of P. 13155, but the presence of a vertical inner rib cannot be ascertained. The overlapped area is conspicuous, but it frequently appears to be more extensive in the anterior



TEXT-FIG. 29.—*Etheretmon valenticum*, gen. et sp. nov.  
Median dorsal ridge-scales. [P. 13159.  $\times 12$ .]



flank-scales than is actually the case, owing to the telescoping of the pectoral region which has taken place in the majority of specimens.

The dorsal margin is covered by a series of enlarged oval ridge-scales which extend from near the occiput to the dorsal fin (text-fig. 29). In front they are oval and flat, and at first are scarcely larger than the neighbouring body-scales, while the area of overlap is small. Further to the rear a median ridge is increasingly developed, and the scales become large and more pointed behind, while the imbrication deepens and the anterior margin is progressively more indented, so that the hindmost scales are V-shaped. These points are well shown in text-figs. 30 and 31, in the first of which the scales are drawn out, and the overlapped surface



TEXT-FIG. 30.—*Etheretmon valenticum*, gen. et sp. nov.  
More posterior dorsal ridge-scales, somewhat displaced.  
[P. 13150.  $\times 7$ .]



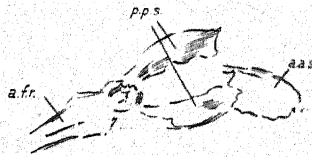
TEXT-FIG. 31.—*Etheretmon valenticum*, gen. et sp. nov.  
Dorsal ridge-scales immediately preceding dorsal fin.  
[P. 13154.  $\times 5$ .]

is visible. The scales are largest just in front of the dorsal fin and then grade insensibly into the anterior rays of the fin itself. The series is continued behind the dorsal fin along the upper caudal lobe, where the scales are very long and V-shaped. These long forms are obviously of a paired origin, and the so-called azygous ridge-scales into which they grade were doubtless of a like nature. A similar series, comprising four scales, runs from behind the anal fin to the lower caudal lobe.

Immediately in front of the anal fin are a pair of very large plates which apparently surrounded the vent. Their upper margin is rounded and the length considerably exceeds the depth (text-figs. 32, 33). In front of these is a smaller plate, apparently unpaired, which is seldom seen, as it is usually obscured by the rays of the ventral fins.



TEXT-FIG. 32.—*Etheretmon valenticum*, gen. et sp. nov. Left posterior anal scale. [P. 13160.  $\times 5$ .]



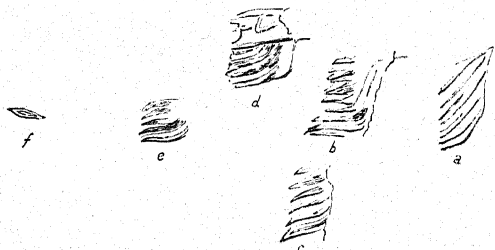
TEXT-FIG. 33.—Anal scales.  
[P. 13161.  $\times 6$ .]

a.a.s. = Ant. anal scale. p.p.s. = Paired posterior scales. a.f.r. = Ant. fin-ray.

The median ventral line from the pectoral fin to the anal-scales is marked by a series of ridge-scales similar to those on the back, but rather more pointed.

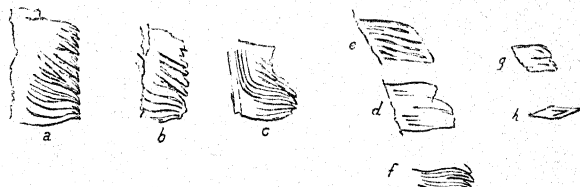
The squamation of most of the specimens is worn and, in consequence, much of the ornament had vanished, greatly changing the aspect of the scale. In addition there is a conspicuous difference between the scale-ornament of the two forms as described above. On the most anterior flank-scales, the ornament is composed of rather irregular, curved diagonal ridges (text-fig. 34a). That of the main flank scales is also composed of diagonal ridges, but these are regular and they number from four to eight according to the position of the scale. In addition, there are rugæ which run vertically in front of the others and then curve round below parallel to the inferior margin. These rugæ are roughly straight in their horizontal portion in the *forma typica*, and they end independently on the hinder margin (text-fig. 34 b-e). In

the variety *ovensii*, however, the inferior margin is decidedly convex, and the lower rugæ curve in a corresponding manner and coalesce to form one or two complex lobes behind (text-fig. 35 a-d). The rugæ in all these scales are really compound and are formed by the junction of two ridges (text-fig. 34 b-c), and the space between is striated. Diminution in the number of rugæ naturally takes place in the shallower scales, and in extreme cases they are simply bilo-



TEXT-FIG. 34.—*Etheretmon valenticum*, gen. et sp. nov. Scales of holotype, P. 13145 [except "f" which is from P. 13161.]

- (a) Sub-ventral, 1st row. (b) mid-flank, 10th row.  
(c) 6th row below lateral line, 12th vertical row.  
(d) Lateral line. (e) Posterior flank. (f) Caudal body prolongation. [ $\times 6$ .]



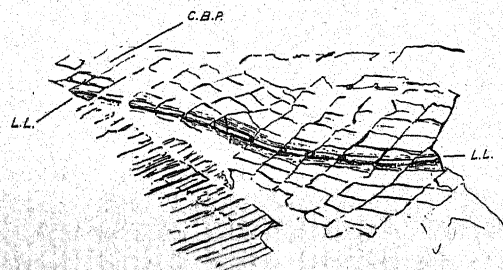
TEXT-FIG. 35.—*Etheretmon valenticum*, var. *ovensii*, nov. Scales of holotype of variety, somewhat worn.

- (a) Anterior flank, 2nd row. (b) Middle flank, 9th row.  
(c) Middle flank, 11th row. (d) Posterior flank. (e) Posterior dorsal. (f) Posterior ventral. (g) Caudal pedicle. (h) Caudal body prolongation. [P. 13176.  $\times 6$ .]

bate (text-fig. 35 g). The scales of the caudal body prolongation to the tip of the tail are ornamented with a median depression (text-figs. 34 f, 35 h).

The ridge-scales are decorated with longitudinal ridges which, in the more oval forms, curve inwards in front and behind to form closed rings.

There are approximately forty-eight vertical rows of scales from the shoulder girdle to the start of the reversed series on the tail (P. 13150, 52, 62), but the number of horizontal rows is not so easily determined; on the pectoral region it is in the neighbourhood of twenty-two (P. 13176).



TEXT-FIG. 36.—*Etheretmon valenticum*, sp. nov. Posterior end of lateral line. [P. 13152.  $\times 5\frac{1}{2}$ .]

L.L.-L.L.=Course of lateral line. C.B.P.=Caudal body prolongation.

Sensory Canals.—The course of the lateral line from the shoulder girdle to the base of the caudal body prolongation can be traced with ease in many specimens. On the tail it turns upwards to run along the lower margin of the body prolongation; but, after reaching the ventral border, the conspicuous ridge on the scales disappears and its course cannot be followed further backwards (text-fig. 36).

The opening of the canal on the surface of the scale is not by a slit or pore, but by an excavation in the posterior border of the scale (text-fig. 36).

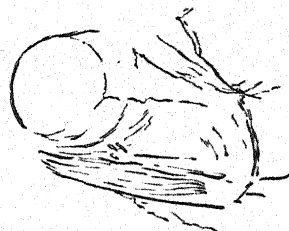
Anteriorly, the main canal passes upwards through the supracleithrum and then forwards along the ventral borders of the post-temporal, tabular, supratemporal, and intertemporal. This is particularly well shown by P. 13154 (text-fig. 21) in which the external layer of the head bones has flaked off, exposing to view the canal filled with calcite. Ordinarily, the canal is not easily seen on the head, as it forms neither internal nor external ridges, and the ornament in any case tends to obscure its course. The suborbital branch is nowhere seen, but part of the supraorbital canal is exposed in P. 13154, though only where it traverses the frontal.



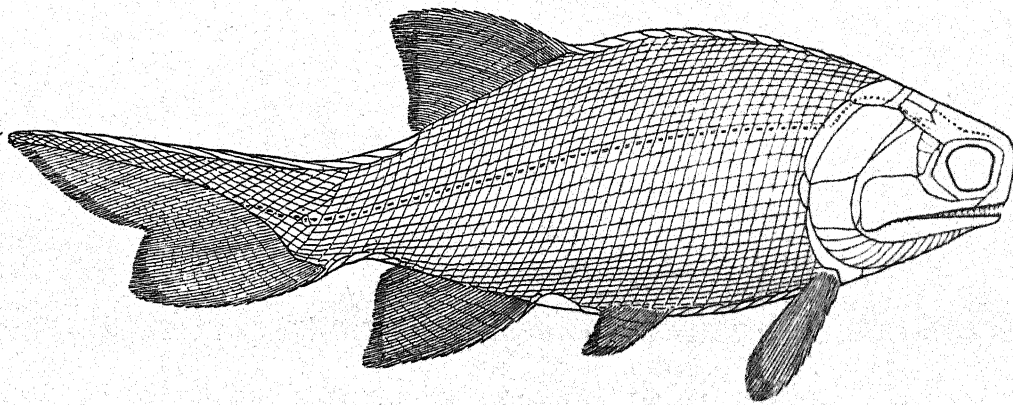
Juvenile Specimens.—There are nine examples of the young stages of this fish and as such they are worth separate notice, although some have been noted in the general description. The largest of these specimens is 5.5 cm. long, and the smallest measures 2.0 cm. less.

Except that the orbit is relatively larger (text-fig. 37) and the fins more developed (P. 13167), they are identical with the adult specimens. Many features are best displayed by these very small fishes, and especially to be noted are the head-bones and scale-sculpture in P. 13163, P. 13170, the unarticulated pectoral fin (P. 13168, P. 13170), and the characters of the ventral (P. 13170), the dorsal (P. 13163), the anal (P. 13162, 4, 7), and the caudal fins (P. 13162, 3, 7).

*Remarks.*—This little fish, of which a restoration is attempted in text-fig. 38, is easily separated from other genera of this family by the characters of the fins, which in shape, size of fulcrum, and the inarticulation of the pectoral rays are unique; and the configuration of the head-bones with the subdivided postorbital series helps further to distinguish this form. In shape it is stout and rather of the "gold-fish" build, resembling in this respect, as well as in size, some of the *Canobii* such as *C. crassus* (TRAQUAIR, 1914, p. 181). The head-bones are normal in shape and arrangement, and except in minor details, such as subdivision of the postorbital, they do not differ greatly from those of the "normal" genera as *Elonichthys*, etc. The dentition is rather poorly developed, for even the lanianaries are small and certainly not fitted for preying on the heavily armoured members of its own class, while its stout build and large, deep fins clearly show that it was not adapted for swift motion such as the pursuit of



TEXT-FIG. 37.—*Etheretmon valenticum*, gen. et sp. nov. Head of young individual. [P. 13158.  $\times 4\frac{1}{2}$ .]



TEXT-FIG. 38.—Restoration of *Etheretmon valenticum*, gen. et sp. nov. [ $\times 2$ .]

other fishes would entail; it is probable that it preyed on the chitinous arthropods in which these waters abounded, and on the soft-bodied creatures of which time has left no trace.

#### Genus STREPHOSHEMA,\* NOV.

Trunk very deeply fusiform; caudal pedicle long and stout. Snout rather pointed, forehead sloping. Head deep with prominent orbit anteriorly placed; suspensorium very oblique, gape moderate. Jaws stout; outer teeth of lower jaw numerous and bluntly styliform; inner teeth large, acutely conical (upper dentition unknown).

Operculum deep and relatively narrow (suboperculum and branchiostegal rays unknown).

\* στρέφειν—to distort; σχῆμα—a shape.



Cleithrum and clavicle very stout. External bones ornamented with interrupted rugæ. Dorsal and anal fin-rays stout and evenly articulated to base, distally dichotomized; those of caudal similar but finer. (Size and shape of dorsal and paired fins unknown.) Anal fin moderate in size, triangularly acuminate, largely posterior to dorsal in position. Tail deeply cleft and very inequilateral. Squamation regular except under dorsal (and also over anal) fin where the scales are subdivided and the rows deflected; line of back and belly marked by series of enlarged median ridge-scales, of which the ventral series is paired. Scales ganoid, thick, rhomboidal; upper front angle of flank-scales, which are deepened anteriorly, much produced; ventral scales very narrow, almost luniform. Scale-ornament composed of conspicuous ridges, disappearing on caudal body prolongation.

This genus contains one species:—

*Strepheoschema fouldenensis*, sp. nov.

(Text-figs. 39–46.)

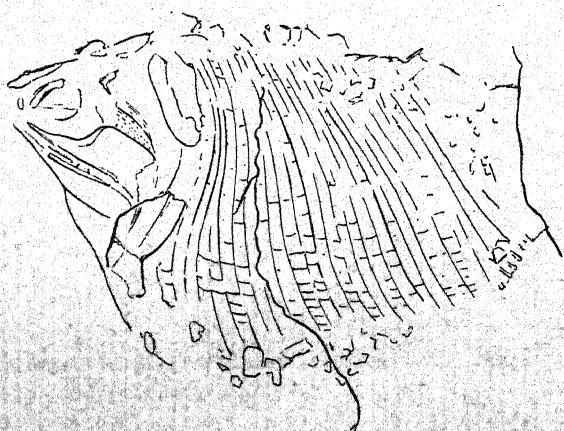
*Holotype*.—Imperfect fish in counterpart, Brit. Mus., P. 13116–7.

*Paratype*.—Three specimens, P. 13118, P. 13119, P. 13191.

*Description of Specimens*.—The holotype consists of the head and trunk of a fish of moderate size, without fins, but nevertheless very beautifully preserved. P. 13118 is the hinder two-thirds of a larger fish crushed dorso-ventrally. The tail and dorsal fin are present in part and, although shapeless as a whole, the specimen shows a number of finely preserved scales.

P. 13119, a piece of worn squamation, is important, as it shows part of the dorsal fin and the neighbouring scales. P. 13191 is the caudal region of a very small specimen, in which the shape of the tail and anal fin is partly preserved.

*Shape and Size*.—The shape is very deeply fusiform and the head correspondingly deep with a sloping forehead and sharp snout, while the throat is full and gradually merges into the body. The length preserved in the holotype as far as the hinder end of the dorsal fin is 7.0 cm., but as the head is bent upwards another 0.5 cm. may be added. The head is 2.7 cm. long and the maximum depth of the body, even when allowing for the displacement of the ventral



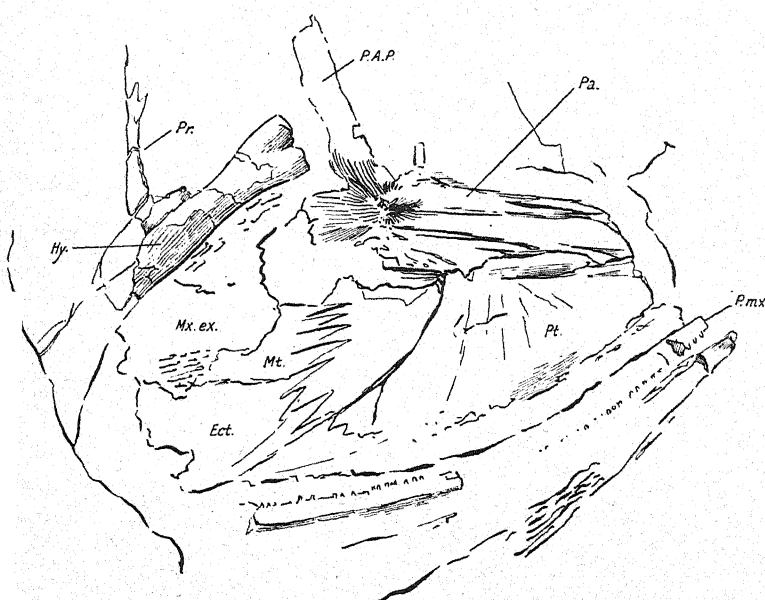
TEXT-FIG. 39.—*Strepheoschema fouldenensis*, gen. et sp. nov.  
Right-hand slab of holotype. [P. 13116. x1.]

scales, is no less than 4.7 cm. The uncrushed state of the pectoral girdle and the position of the dorsal and anal baseoste clearly prove that the considerable depth of this specimen is natural and not due to distortion. The caudal pedicle is long and stout and the extension of the body in the tail elongated. P. 13118 is part of a specimen half as large again as the type, and measures 7.5 cm. from the hinder end of the dorsal fin to the tip of the tail. It was therefore about 17 or 18 cm. in total length.

*Skull*.—(Cranium).—Except for a doubtful fragment of a basiptyergoid process, nothing is to be seen of the substitution-bones; and, of the membrane-bones, the parasphenoid alone is well preserved. This bone lies on the left-hand slab (text-fig. 40) and shows the aboral surface. It is crushed and the posterior border is broken away, although there cannot be a great deal missing. The bone is short and broad and narrows towards the front. The im-

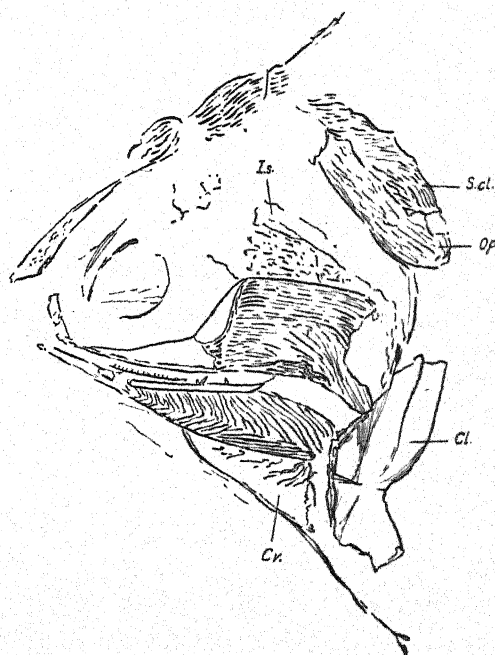
perfect remains of a long and powerful ascending process are preserved on the left side, and at the base of this in the middle of the parasphenoid is a conspicuous but irregular pit for the hypapophysis; here also was the centre of ossification (see STENSIÖ, 1921, p. 176). In front of this the bone is flat, but the sides are slightly turned down, so that in this case it is the oral surface that is concave. A pair of longitudinal grooves run forwards from the median pit on either side of the central flattened area, increasing in depth as the anterior margin is approached. These are flanked by a fainter pair which meet the first where they cut the front margin of the bone.

The outlines of the cranial roof-bones are in every case obscured, but the ornament can be seen in the holotype, and is composed of irregularly longitudinal rugæ which are much



TEXT-FIG. 40.—*Strepheoschema fouldenensis*, gen. et sp. nov. Visceral skeleton, etc. of holotype. [P. 13117.  $\times 4\frac{1}{2}$ .]

Ect. = Ectopterygoid. Hy. = Hyomandibula. Mt. = ? Metapterygoid. Mx. ex. = Maxillary expansion. Pa. = Parasphenoid. P.A.P. = Ascending process of parasphenoid. P.m.x. = Premaxilla. Pr. = Process from hyomandibula. Pt. = Pterygoid.



TEXT-FIG. 41.—*Strepheoschema fouldenensis*, gen. et sp. nov. Head of right-hand slab of holotype. [P. 13116.  $\times 2$ .]

Cl. = Cleithrum. Cr. = Clavicle. Is. = Impression of suspensorium. Op. = Operculum. S.Cl. = Supracleithrum.

interrupted, and anastomose frequently. The position of the orbit is indicated in P. 13116 (text-fig. 41). It is large and, as usual, placed far forward and low down.

(Visceral Skeleton.)—The greater part of the palate lies spread out beneath the parasphenoid in P. 13117 (text-fig. 40). It is crushed flat and the upper hinder portion is obscured by the maxillary expansion. The palatal region in palæoniscids was exceedingly difficult to interpret until a complete series linking the extreme forms with that of the osteolepids was described by D. M. S. WATSON (1925, p. 851). The palate of *Strepheoschema* seems to be nearest to that of *Elonichthys caudalis* in that it is chiefly composed of a large pterygoid, and that the autopalatine and the suprapterygoid series, except for a doubtful portion of the metapterygoid, are missing (*ibid.*, p. 856, text-fig. 25). The upper margin of the pterygoid is thickened and smooth, so that it stood freely in the skull; it bears two notches, of which the one far forwards is difficult of interpretation unless it were connected with a palatal nostril (WATSON, 1925, p. 859); while the second is for the passage of the 2nd and 3rd branches of the trigeminal

nerve. This second notch is unfortunately broken, but from it there runs a deep groove which most likely marked the course of the maxillo-mandibular vein (ALLIS, 1922, p. 262). Just before this groove crosses the suture between the pterygoid and the ectopterygoid, it is joined by a smaller branch from the outer edge of the pterygoid, and this doubtless indicates the course of the maxillary ramus. The suture between the ectopterygoid and the pterygoid is remarkably jagged, but is less so than that between the pterygoid and the doubtful metapterygoid. The identity of the latter bone is questionable on account of the uncertain nature of the suture with the ectopterygoid; it might be a crack, in which case the whole is a very large ectopterygoid.

The outer margin of the palate is turned upwards and outwards towards the maxilla, but along the groove thus formed the bone is so badly fractured that the identification of the palatine series is impossible, and no teeth are to be seen.

Lying obliquely behind the bones described above is the powerful hyomandibula. The upper half of the bone is actually present, but below the middle it is shown in impression. The upper end, which is imperfect, is normally expanded and bears a short median groove. About the middle of the hinder face of the bone an outgrowth is given off very much as is the *processus opercularis* in *Boreosomus* (STENSIÖ, 1921, p. 211, text-fig. 70); but it is irregular and has the appearance of being diseased, for it bears at least three crater-like scars. Instead of being short as in *Boreosomus* it apparently continues into a long slender process, as long as the upper half of the hyomandibula itself (*Pr.*, text-fig. 40). The process is expanded at the distal end where it is broken away. There is a distinct crack where it joins the hyomandibula, but it is certainly part of that bone. Distinctly abnormal, it is in all probability an ascending process in a diseased state, and consequently it has suffered hypertrophy. This view is supported by the pathological condition of the base.\*

The preoperculum covers a large area of the cheek, but the upper margin is obscured by the impression of the hyomandibula. It is of the usual bent shape and the anterior expansion is very deep (text-fig. 41). The operculum is obliquely rhomboidal and measured  $1.0 \times 0.5$  cm. All traces of the suboperculum and the branchiostegal rays are obliterated by the pectoral girdle.

The ornament of the preoperculum consists of rather irregular, elongated tubercles or short rugæ, and that of the operculum of interrupted, longitudinal striæ, which are shortest along the posterior border.

The maxilla is of the usual pattern, but the rectangular posterior expansion is exceptionally deep, and the oral-margin is much turned down at the hinder end. The foremost part of the suborbital bar is very narrow, though it expands somewhat under the postorbital series. There is a horizontal flange directed inwards along the oral margin, but none of the teeth it bore is now to be seen. The mandible is moderately long, quite slender in front, and greatly deepened behind.

The ornament of the maxillary expansion is composed of fine, anastomosing rugæ which run parallel with the upper and hinder margins; and that on the suborbital bar, although indifferently preserved, appears to have been tuberculated and is quite abruptly separated from that of the expansion. There is a broad, smooth area on the orbital margins of both portions, where the bone was overlapped by the circum- and post-orbital elements. The mandible is decorated with numerous fine rugæ running backwards and downwards until underneath the jaw they are abruptly deflected forwards.

\* Professor D. M. S. WATSON suggests that this "process" may be the result of ossification in the *musculus adductor hyomandibularis*.

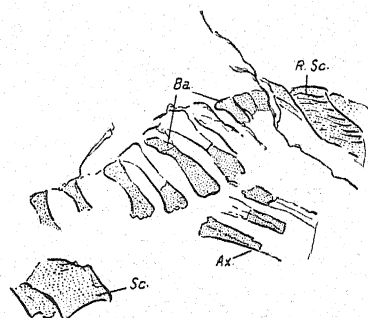


Dentition.—Except for a few shapeless fragments seen on the premaxilla on the left-hand slab of the holotype, nothing is known of the upper dentition.

The right mandibular ramus is divided between the two slabs, the right bearing part of the dentigerous oral shelves and a complete impression of the outer surface, while the left shows the remainder of the shelves of the dentary and pre-articular and the crushed remains of part of the mandible itself. The shelves are separated and lie across one another. The dentary bore conical lanianries of which three are still preserved (P. 13116), while the inner bone is seen on both slabs supporting a series of numerous small, blunt, and evenly spaced teeth. There are no signs of any coronoid elements, and, as described, the teeth seem to have been borne on the horizontal flanges of the dentary and pre-articular (see WATSON, 1925, p. 861).

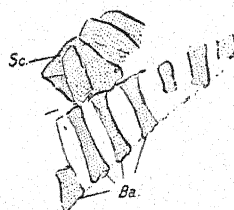
Axial Skeleton.—This is entirely wanting.

Unpaired Fins.—There are no lepidotrichia preserved in the holotype, but parts of the dorsal fin are shown by P. 13118 and P. 13119 (text-fig. 44), of the caudal by P. 13118 and P. 13191, and nearly all the anal by P. 13191. The lepidotrichia are very broad and rather closely and evenly articulated; except, of course, that the basal segment of the caudal rays is longer than the others. Each ray has an ornament of fine diagonal striae.



TEXT-FIG. 42.—*Strepheoschema fouldenensis*, gen. et sp. nov. Dorsal radials. [P. 13117.  $\times 3\frac{1}{2}$ .]

Ax. = Axonosts. Ba. = Baseosts.  
R.Sc. = Ridge-scales. Sc. = Scales.



TEXT-FIG. 43.—*S. fouldenensis*, sp. nov. Anal radials. [P. 13116.  $\times 4\frac{1}{2}$ .]

Ba. = Baseosts. Sc. = Scales.

The dorsal fin is very imperfect in each case, and its shape cannot be determined. At least twenty-nine rays are present in P. 13118. The small specimen P. 13191 shows that the anal fin was triangularly acuminate in shape and well-developed, with upwards of thirty rays; doubtless the dorsal was of similar proportions and form.

The occurrence of the radial series in the holotype fixes the position of the fins. Both were rather posteriorly placed, as the dorsal arises behind the middle of the back on the downward slope of the dorsal contour, while the origin of the anal is slightly more posterior in position, the fins being partly opposed. The dorsal baseosts (text-fig. 42), of which there are eight, are very imperfect and preserved in part as impressions. The anterior bones, which measure 2.5 mm. in length, are flat and slender and have a slight constriction about their middle. To the rear, the baseosts become shorter and shaped more like an hour-glass, while their length dwindles uniformly until the last one preserved has only half the length of the foremost. Since the radial and lepidotrich series are coextensive in this family, an idea of the base length of the fin could be obtained from the measurement of this series, were it complete. It is only 1.0 cm. long, however, making the fin rather short-based. This is unlikely as the anal was normally well-developed, and generally in such cases among palæoniscids the two fins are of similar dimensions. It is probable, therefore, that the hindmost baseosts are not preserved

in this specimen. The axonosts, of which only two and the impression of a third remain, underlie the anterior baseosts conformably. They are shorter and less expanded at the end than are the distal elements. A considerable part of the baseost series of the anal fin is exhibited by P. 13116 (text-fig. 43). Like those of the dorsal they are fragmentary, and the full length of the anterior baseosts is not shown. They are similar to the corresponding ossicles of the dorsal fin and vary in the same way, except that the last one or two are rather stouter. Seven are actually preserved in part, and the impressions of three more anterior elements are just discernible on this slab and the counterpart. There are no signs of any anal axonosts.

The tail is largely preserved in the small fish P. 13191. It is very inequilobate and deeply cleft, and the upper lobe is long and slender. In this specimen the distal dichotomy of the rays is very well shown.

The presence of fulcra in the median fins cannot be detected for certain, but on both anal and caudal fins in P. 13191 there are indications that such were present.

Paired Fins—(Pectoral Girdle).—The post-temporal plates are large and oval, and the supracleithra are of the usual elongate form.

The cleithrum is extremely large and powerful. The greater part of the bone is shown from the inner aspect by P. 13116 (text-fig. 41) in a quite uncrushed condition, and impressions of the outer surface of the missing parts are also present. The upper vertical lamina is divided by a median ridge or fold into two halves, the anterior of which points forwards and inwards to the branchial cavity (*cf.* TRAQUAIR, 1877, p. 25). The horizontal basal portion is very broad and gently rounded and, as the curvature is preserved, it shows that the fish was quite thick-bodied and by no means absolutely flattened from side to side. The uncrushed state of this bone proves that the great depth of the fish is natural, for the lower contour is continued by the displaced ridge-scales of the belly. In P. 13117 there is the impression of a small post-cleithral scale.

All the bones of the pectoral girdle are ornamented externally with rugæ which are generally interrupted. On the post-temporals, however, they are whole and frequently anastomose. On the supracleithrum the rugæ are roughly longitudinal, but the pattern is interrupted by the lateral line which follows its usual course. The ornament of the cleithrum runs somewhat obliquely and becomes broken up along the posterior border, while that of the clavicle, as far as can be seen, is wholly tuberculate.

(Fin.)—There is nothing left of the fin itself in any specimen, but it was probably large, in keeping with the powerful cleithrum which is deeply notched behind for its reception.

(Ventral Fin.)—This is entirely missing in every specimen.

Squamation.—The scales are extremely thick and covered with brilliant ganoine.

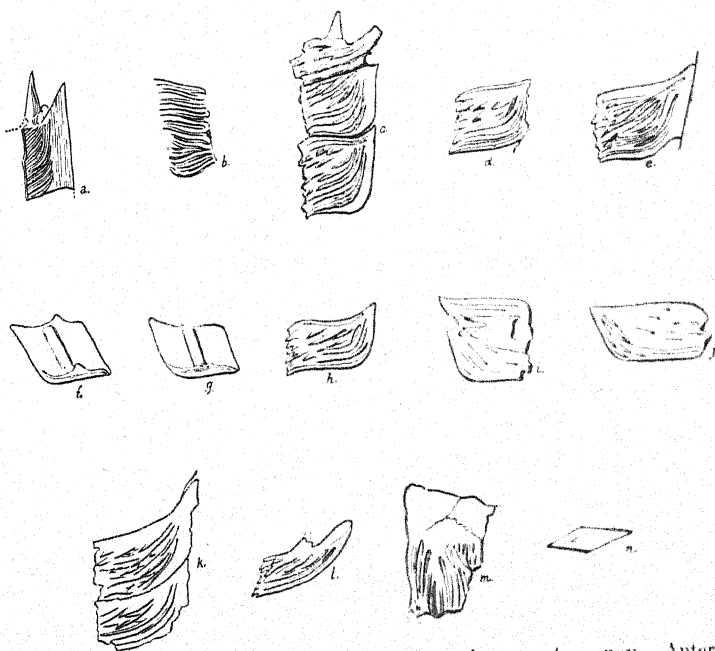
The variation in the squamation is normal for the family, except that under the dorsal fin the scales are subdivided and the rows deflected upwards (text-fig. 44). A similar arrangement doubtless existed over the anal fin as well, but this region is in no case preserved. The anterior flank-scales are considerably deeper than broad, but dorsally and to the rear the scales become rhombic, while ventrally they are very much wider than deep. A conspicuous inner rib is present as well as a strong peg-and-socket articulation; the latter feature, however, disappears caudally. The upper and lower borders are sigmoidally curved and the hinder is denticulated. The number of posterior denticles naturally diminishes with the decrease in depth of the scales, of which those that are under the dorsal fin are smooth behind. The upper front corner is considerably produced, especially in the anterior scales on the flank and belly: indeed on the latter they are in many cases almost luniform in shape. The area of overlap is large except in the more posterior flank-scales; for, like the articulations, this also

tends to disappear towards the tail. The ventral scales, and to some extent the anterior flank-scales, have, in addition, a conspicuous dorsal area of overlap.

Along the ventral line in both P. 13116 and P. 13118 are a number of greatly enlarged scales, twice the size of those on the flank. They have a special ornament and an extraordinarily large area of overlap. These scales vary in sculpture and size, the most anterior being the smallest (P. 13118); unfortunately not one is completely preserved. In shape they are rhomboid so that they cannot be azygous, and they are peculiar in that the smooth dorsal margin encroaches more and more on the denticulated posterior border until the latter is almost completely wanting in the rearmost scales. It seems that these constitute a series of paired ridge-scales of a rather special type. They commence immediately behind the pectoral girdle,



TEXT-FIG. 44.—*Strepheoschema fouldensis*, gen. et sp. nov. Dorsal fin-rays and scales. [P. 13119.  $\times 6\frac{1}{2}$ .]



TEXT-FIG. 45.—Scales of *Strepheoschema fouldensis*, gen. et sp. nov. Anterior (a-b), middle (c) and posterior (d-e) flank-scales. Inner view of flank-scales (f-g). Posterior inferior flank-scale (h). Scales of caudal pedicle (i-j). Anterior (k) and middle (l) ventral scales. Fragment of paired ventral ridge-scale (m). Scale of caudal body prolongation (n). (c) and (i) show lateral line. [a, c, d, e, h, and k from specimen P. 13117; b, f, g, and m from P. 13116; i, j, l, and n from P. 13118. All enlarged  $\times 5-6$ .]

but their backward extent is not shown—they do not extend behind the anal fin for there the ridge-scales are smaller and are of the usual azygous form.

A series of the ordinary, unpaired ridge-scales also marks the line of the back, and extends along the dorsal margin of the tail.

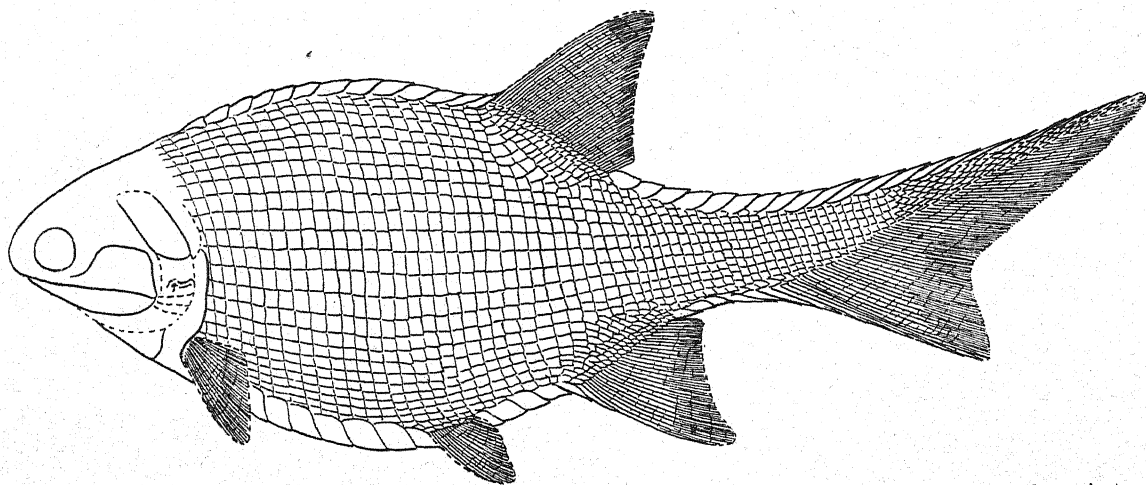
The ornament of the scales is characteristic (text-fig. 45). The chief feature is a series of prominent, flat rugæ which run obliquely from the top front corner. As a rule they do not completely traverse the surface of the scale, but end at irregular intervals in sharp points. In front of and below these is another series which runs parallel to the front and lower margins, and in some of the deeper scales, especially the large paired ridge-scales, a strong ruga also forms the upper margin of the scale. The ornament is more irregular in the paired ventral ridge-scales, and the diagonal rugæ cross one another in trellis-work fashion. Posteriorly, the diagonal rugæ on the flank-scales become rather broader, and the points in which they end have the form of arrow-heads; while on the tail the ornament degenerates into fine striæ



and elongated pits. Only a single median pit remains on the diamond-shaped scales of the body prolongation.

Sensory Canals.—The course of the lateral line is normal as far as can be ascertained, and the canal opens on to the surface of the scales by a slit situated about two-thirds of the way across (text-fig. 45*i*).

Remarks.—The most striking feature of this fish is the great depth of the body (see Restoration, text-fig. 46), recalling types seen in many other families of Actinopterygians, but not hitherto described in the *Palæoniscidæ*.\* In this character *Strepheoschema* approaches the *Platysomidæ*. In all other respects, such as the position of the orbit, the deeply cleft



TEXT-FIG. 46.—*Strepheoschema fouldenensis*, gen. et sp. nov. Restoration. The shape of the paired fins is entirely conjectural.

mouth, jaws, etc., it is a typical palæoniscid as much as is *Gonatodus*, which is the next deepest member of the family. There is, however, little else that is common to these two genera except that both have blunt teeth; here again they differ, however, for those of *Strepheoschema* are quite uncurved and are accompanied by ordinary conical lanianries, a combination unique in the family.

#### SUMMARY.

As was hinted in the introduction, the main interest of this collection is stratigraphical, for a relatively extensive fauna as this from such barren rocks is certainly welcome; but from the palæozoölogical standpoint, the specimens are a little disappointing. The larger fragments are of no palæontological importance, and the new species of *Acanthodes* is of systematic interest alone; but the new palæoniscids raised the hope that here we might glean some new anatomical facts concerning the skull from fishes of a critical period in the evolution of their order.

STENSIÖ's work on Triassic palæoniscids (1921) and WATSON's on those of Coal Measure and Devonian Age (1925) have vastly increased our knowledge of the anatomy and affinities of these fishes, and facts concerning the intermediate genera of Lower Carboniferous times would have been extremely welcome. The crushing undergone by these new fishes has, however, destroyed all chance of any such information coming to hand. As new genera these fishes have a systematic value, for they add four more forms to the already prodigal number of permutations on the palæoniscid theme, and some of them, by reason of their extreme characters, are well worthy of attention.

\* *Benedius* is a true *Platysomid* according to G. A. BOULENGER (1890).

*Fouldenia* is interesting on account of the peculiar shape of the preopercular and maxillary bones, and the condition of the fin-rays in this genus seems to throw light on the nature of fin-fulcra in other genera. In this case, the free distal end of each of the anterior graduated rays is expanded and covered with ganoine, greatly resembling the series of fulcra usually found in members of this family and serving the same purpose, namely to strengthen the cut-water. Doubtless for mechanical reasons it was more advantageous to have a greater flexibility of the anterior fin-margin. This required that the expanded ends of the rays should be smaller and more numerous, and therefore, that more of the anterior rays should enter the graduated series; but even so the necessary flexibility would not be achieved if all retained their connection with the base. This is precisely the condition found in *Fouldenia*, in which the graduated series is long and the maximum depth of the fin is relatively far behind. The next condition, therefore, was the loss of the basal attachment by a number of rays, and the consequent development of the fulcra therefrom by reattachment to such of the anterior lepidotrichs as remained in normal connection with the baseoste. In *Aetheretmon* this intermediate stage is beautifully shown, for the fulcra are few and are very long; they are not greatly differentiated from the normal rays and cannot have long lost their basal connection. From this stage it is not difficult to derive the forms of fin in which the anterior border is protected by the customary series of fulcra of various sizes. Obviously the number of anterior rays which could have been absorbed into the fulcral series is limited, and presumably, therefore, the large series of minute fulcra seen in many genera are derived by subdivision.

It is not suggested that *Fouldenia* was itself ancestral to the genera with the more advanced type of fulcra, for in the Middle Old Red Sandstone genera *Cheirolepis* and *Stegotrachelus* (WOODWARD and WHITE, 1926) separate fulcra were well-developed and were, in the latter, of small size. Nevertheless it gives a strong clue to the mechanical origin of fulcra which may have been developed independently several times in widely different branches of the family.

*Carboveles* provides another interesting instance of the degeneration of the squamation among ganoids which anticipated and even outran the diminution in armour that must have generally taken place in this group in early Mesozoic times, when the teleost type was evolving. In the retention of the squamation it showed a nearer parallelism to that change than did *Phanerosteon*, to which it is obviously nearly allied. The latter may represent the extreme phase of this change and be the direct descendant of *Carboveles*, for *Phanerosteon* is so far known only from the Oil Shale Group of Eskdale, Dumfries-shire, an horizon of considerably later date than that of Foulden.

Besides the fulcra noted above, *Aetheretmon* exhibits other features worthy of notice. The inarticulate condition of the pectoral fin is remarkable. That the first one or two rays should be without articulation is usual as it occurs in a number of palæoniscids, the fins being merely balancers (see WATSON, 1925, p. 824). But that the whole fin should have been stiff is most unusual, for the ganoid rays of these fishes must have lacked the suppleness of the lepidotrichs of modern forms.

Lastly, the form of *Strepheoschema* is certainly the nearest approach that a palæoniscid ever made, so far as we know, to a platysomid. But it is not a platysomid nor, even for that matter, can it be regarded as a connecting link, for the form of the head-bones is typically palæoniscid and far removed from the physiognomy of the platysomids of the Lower Oil Shales.

Although the Foulden strata are almost at the very base of the Carboniferous rocks, and their fauna must certainly be the earliest with any considerable series of fish remains described from that formation, yet it must be held that the palæoniscids do not show any markedly



primitive character. This is not to be expected, for in the Middle Old Red Sandstone genus *Stegotrachelus* (WOODWARD and WHITE, 1926) which is the earliest member of the family with normal squamation,\* the primitive features are by no means striking. We have to go still farther back to find a likely ancestral form with sufficiently generalized characters to be of real interest and to throw light on the origin of the Actinopterygians.

About the other organisms associated with the fishes little can be said; the plants have been partly worked out, as mentioned in the introduction, by Dr KIDSTON, and a summary by my colleague, Mr W. N. EDWARDS, is here appended. The Molluscs are not determinable, and with the exception of the problematical *Glyptoscorpius caledonicus* Peach, the identifiable Arthropods are confined to two genera of doubtful species, *Tealliocaris* and *Crangopsis*.

It is an interesting assemblage, especially as it is the earliest Carboniferous fauna described from Britain, and it is hoped that more material may be collected which will throw further light on the life of this early period.

\* This excludes *Cheirolepis* of the same age, which by reason of its aberrant squamation is scarcely likely to be on the main line of development, and may be referred to a separate sub-family.

#### LIST OF FOSSILS FROM FOULDEN.

##### PISCES.

*Acanthodes ovensi*, sp. nov.  
*Gyracanthus*, sp.  
*Callopristodus pectinatus* (Agassiz).  
*Rhizodus hibberti* (Agassiz and Hibbert).  
*Strepsodus*, cf. *sulcidens* (Hancock and Atthey).  
*S. striatulus* Traquair.  
*S.*, sp.  
*Fouldenia ottadinica*, gen. and sp. nov.  
*Carboveles ovensi*, gen. and sp. nov.  
*Ætheretmon valenticum*, gen. and sp. nov.  
*A. v.* var. *ovensii*, nov.  
*Strepheoschema fouldenensis*, gen. and sp. nov.

##### ARTHROPODA.

*Glyptoscorpius caledonicus* Peach.

*Tealliocaris*, sp.

*Crangopsis*, sp.

##### MOLLUSCA.

*Gasteropoda*, indet.  
*Lamellibranchiata*, indet.

##### PLANTÆ.

*Aneimites acadica* Dawson.  
*Sphenopteris (Telangium) affinis* Lind. and Hutt.  
*Ootheca globosa* Kidston.  
*Cf. Coseleya*, sp.  
*Carpolithus*, sp.  
 Fructification of Pteridosperm.  
*Lepidodendron*, sp.

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## APPENDIX.

## LOWER CARBONIFEROUS PLANTS FROM FOULDEN, BERWICKSHIRE.

By W. N. EDWARDS, B.A., F.G.S., of the British Museum (Nat. Hist.).

The plant remains in the THOMAS OVENS Collection from Lower Carboniferous (Tuedian) rocks near Foulden, Berwickshire, are of considerable interest, though few species are represented. Some have already been described by KIDSTON, to whom OVENS had sent many of his best specimens, and these are now in the KIDSTON collection at the Museum of Practical Geology, Jermyn Street. In addition to those mentioned below, there are branched fragments of Pteridosperm rachis, impressions of larger stems, and some other obscure specimens. Numerous examples of *Spirorbis* occur on the plant remains.

*Aneimites acadica* Dawson.

This frond has been described and figured by the late Dr KIDSTON (*Mem. Geol. Surv. Gt. Britain, Palæontology*, vol. ii, pt. 5, 1924, p. 414, pl. cx, ff. 4-7). It is the commonest plant at Foulden (B.M. Geol. Dept., V. 16860-64), though it is very rare in Britain, and is confined to the Cementstone group. KIDSTON gave the locality as "left bank of Crooked Burn, about 50 yards below Newton Farm, Foulden, Berwickshire," and the horizon as "near base of the Cementstone group" of the Calciferous Sandstone Series.

*Sphenopteris (Telangium) affinis* Lind. and Hutt.

This pteridosperm frond (V. 16865) has previously been recorded only from the oil-shale group the Calciferous Sandstone, where it is abundant.

*Ootheca globosa* KIDSTON.

Fructifications which are "probably the microsporangia of Pteridosperms" were described by KIDSTON as *Ootheca globosa* (*op. cit.*, pt. 4, 1923, p. 371, pl. lxxi, figs. 6, 6a) from a single specimen found at Foulden.

Cf. *Coseleya*, sp.

Another pteridosperm fructification, also probably microsporangiate, was figured under the above name by KIDSTON (*op. cit.*, pt. 4, 1923, p. 370, pl. lxxvi, figs. 7, 7a), and on a piece of shale in the OVENS collection (V. 16888) are three groups of sporangia of the same type. *Coseleya* is otherwise known only from the Westphalian, and it seems improbable that the Foulden specimens really belong to that genus.

## Fructification of a Pteridosperm.

Some specimens of a much larger fructification, and of some seed-like bodies, will not be described in detail here, since there are numerous better examples in the KIDSTON collection, which will doubtless be described in a forthcoming volume of the *Survey Memoirs*, when KIDSTON's work is completed. The KIDSTON collection also contains some specimens which may provisionally be referred to as *Carpolithus* sp.

*Lepidodendron*, sp.

A single fragment of a stem showing structure (V. 16870) apparently belongs to the genus *Lepidodendron*. It is interesting as evidence of the occurrence of petrified material at Foulden. Impressions of lepidodendroid twigs (V. 16872) occur in a coarse sandstone matrix, and in the shale are isolated megaspores (V. 16871) like those of *Lepidostrobus*, with capitate appendages.



XII.—The Structure of the Disturbed Deposits of Møens Klint, Denmark.\* By George Slater, D.Sc., D.I.C., A.R.C.S., Imperial College of Science and Technology, London. Communicated by Dr G. W. TYRRELL. (With One Plate and Three Text-figures, including Map.)

(MS. received November 29, 1926. Read January 10, 1927. (Issued separately June 2, 1927.)

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I. INTRODUCTION.

In the summer of 1925 I paid a visit to Møen, a Danish island situated about 50 miles south of Copenhagen, for the purpose of studying the cliff sections.

The particular object of the investigation was to ascertain how far the structure of the disturbed deposits of Møens Klint corresponded with that of the disturbed deposits of the Hadleigh Road Area, Ipswich (17, 20, 23), where the structure is strikingly analogous to that seen in Arctic glaciers; and, further, to ascertain whether the laws of structure formulated from the combined study of Arctic glaciers and disturbed glacial deposits were applicable to the Danish sections (21).

During a preliminary traverse of the area I was accompanied by Mr V. HINTZE, Inspector of the Geological and Mineralogical Museum, Copenhagen, and Mrs E. MERTZ of the Danish Geological Survey, thanks to the courtesy of the Director, Dr V. MADSEN.

The Hotel Hunosøgaard proved a suitable headquarters, and a convenient centre from which to study the cliffs.

II. THEORIES OF THE STRUCTURE.

The classical sections of Møens Klint are perhaps the finest examples in the world of those disturbances which have been attributed by some geologists to ice-action. The theory of the structure, however, has always been a subject of controversy. Neither LYELL nor BONNEY agreed with the ice-theory, the former in 1837 attributing the structure to post-glacial (1 and 5), the latter in 1899 (14, 15) to pre-glacial earth-movements. The investigation of the area has been primarily in the hands of Danish geologists, notably PUGGAARD, whose commendable work on Møens Geologie was published in 1851 † (3).

\* Part 8 of Thesis approved for the Degree of Doctor of Science in the University of London.

† There are two copies of this work in the Library of the Geological Society of London.



One of the earliest workers, FORCHHAMMER, appears to have attributed the disturbances to the combined effects of ice-action and earth-movements associated with volcanic phenomena (2). PUGGAARD's views, which explain the structure by earth-movements, have been concisely summarised by LYELL (5). During the latter half of the nineteenth century there was a strong tendency amongst Danish geologists, notably JOHNSTRUP, to accept ice-action as the most reasonable explanation of the disturbed structure seen in Møen and also in the island of Rügen (4, 6, and 7). In recent years, however, the balance of opinion in Denmark has changed in favour of the hypothesis that the disturbances are due to earth-movements and only to a very limited and superficial degree to ice-action. Mr V. HINTZE is a strong upholder of this view as applied to the Møen sections (16, 19). This hypothesis, in my opinion, is entirely untenable.

In spite of the fact that the Møen sections are on a scale ten times greater than the Ipswich sections, nevertheless it will be shown that the general principles of structure in both areas agree so closely, that there can be little doubt that the whole of the Møen disturbances are due to ice-action. Further, that when the area has been mapped by the Danish Geological Survey, Møens Klint promises to reveal one of the most elegant and instructive examples of glacial tectonics to be seen in the world.

Many of the difficulties raised against the ice-theory appear to be due to a lack of knowledge of the principles of glacial tectonics. As these are the result of recent investigations, the time seems opportune for a concise statement of these principles, so that we may determine in what respects they promise a solution to the complicated structure of Møens Klint. The fundamental laws of structure of the behaviour of ice when meeting with obstructions to movement were formulated by the American school of glaciologists from a study of Greenland glaciers between the years 1890-1900 (8, 9, 10, 13). The application of these principles to disturbed Pleistocene drift deposits has been carried out by me, and this has led to the discovery of further laws of structure. The crucial test of the general application of these laws now appears to me to lie in the Møen area.

### III. GENERAL PRINCIPLES OF GLACIAL TECTONICS.

The general principles of glacial tectonics enunciated below have been formulated from two lines of investigation:

1. The study of Arctic glaciers.
2. The study of disturbed deposits of Pleistocene drift. This combined study has shown that glacial disturbances belong to two great types, A and B, each being marked by particular characteristics, but each class has principles of structure in common.

*Class A*, "the *roche-moutonnée* type," is associated with a forward movement or advance of the ice.

*Class B*, "the *stagnant-glacier* type," is characteristic of retreating ice during the period of deglaciation.

These two classes will be described separately.

*Class A. The Roche-moutonnée Type.*—The chief points of structure in this class are as follows:—

1. The initial cause of the disturbances is the *roche-moutonnée* "core."
2. The superimposed beds dip in opposite directions on the two limbs of the "core."

3. The iceward limb is associated with thrust-planes, and squeezed anticlines or flow-overfolds.

4. The leeward limb is associated with tip-structure, and flow-curves which take the form of drawn-out lenticles.

In disturbances of this type the deposits not only show a definite arrangement both vertically and horizontally, in transverse sections, but they also show a definite tectonic structure when geologically mapped. This I have shown in the Ipswich area. The "cores" form ridges or mounds, and these rapidly vary in trend over small distances according to the directions of pressure and movement operative at the time of formation of the disturbed deposits. This leads to the formation of domes or ridges and a series of spoon-shaped basins. The final result of these movements is the infilling of the basins and the formation of a new topographical feature, in some cases resembling the drumlin-form.

It is to this type that I ascribe the disturbances of Moens Klint, as well as the well-known sections of the Norfolk coast of England.

The thickness of the disturbed deposits as now seen depends upon the following factors:—

1. The volume of the ice.
2. The nature of the country rock. The lithology most suitable for moulding by ice-action appears to be chalk and clay, the least suitable, sand, but deposits consisting of thin beds of clay intercalated with sand are eminently suitable. This has been shown to be the case in Alberta, Canada.

In the *roche-moutonnée* type the material involved in the disturbances has been very largely, if not entirely, transported and re-arranged.

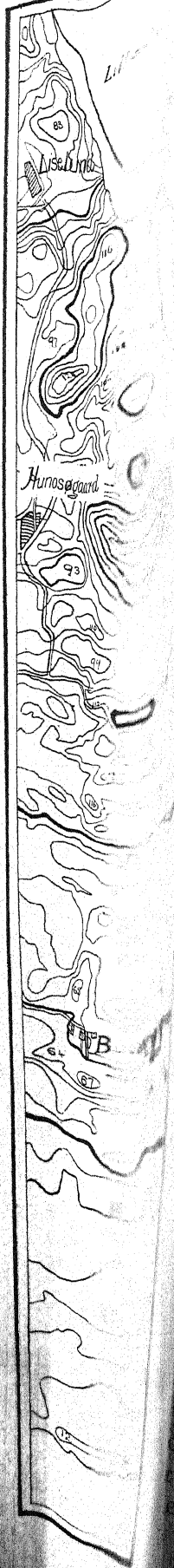
*Class B. The Stagnant-glacier Type.*—The chief characteristics of this type are as follows:—

1. The disturbed beds have a uniform direction of dip, although the amount of dip varies progressively when the beds are traced across the area.
2. Hence the structure is confined entirely to phenomena associated with the iceward-side of an obstruction, this obstruction being the stagnant frontal layers of the overloaded ice-sheet. Thrust-planes are accordingly well developed throughout, and anticlines formed in the hindmost part of the deposits.
3. One of the most remarkable characteristics of this type is the constant repetition of the same dual-deposits. A composite sheet of deposits, such as "clay and sand," has been lifted from the floor of the glacier, transported, and then cut up into lengths, often of almost equal size. These lengths have then been inclined against an obstruction at various angles, and each unit (or pair) is separated from the adjacent pair by a thrust-plane. "Many boards have been cut from the same plank." This type of structure is therefore analogous to the Highland imbricate-structure. The Mud Buttes of Alberta, Canada (24), and the Lønstrup sections provide excellent examples of this type of structure.

In general structure this class of disturbed drift deposits is strikingly analogous to that developed in a stagnant ice-sheet, although in modern Arctic glaciers the structure can only be partially seen, and then usually only on a small scale in sections near the termination of the glacier.

*Principles of Structure common to both Types.*—In addition to the features of structure enunciated above, the following are common to both types A and B:—

1. Disturbances due to glacial action are invariably local.
2. They are always superficial.



bed beds show anomalous dips and strikes at variance with those of the surrounding country rock.

For the structure a considerable overburden is necessary, as the disturbances "structure" in zones of great pressure. If this structure was due to earth-quake overburden would be rock, and the amount of time necessary to remove the material by the type of folding would be insufficient in post-glacial times. On the other hand, if the structure is due to ice, the overburden is provided by a mass of comparatively the englacial material, and the difficulty therefore disappears. flow-overfolds simulating squeezed anticlines occur in association with the vicinity of "horsts."

There has been differential, the upper layers of material moving more quickly than the lower which are associated with frictional phenomena. The thickness of the overburden moving as an entity varies from an inch to many feet.

The sequence between cause and effect can be traced, not only between adjacent sections but out the whole structure when traced backwards; that is, in a direction opposite to the direction of movement, and accordingly in a direction towards the supply of material incorporated of considerable importance is the definite and ordered changes in the position of the thrust-planes, the range being from a low angle to a nearly vertical position, the angles on the iceward side being greater.

The greatest amount of compression is evidenced in the zone of latest formation of the structure, that is, nearest to the source of origin of the material involved.

The topography of a glacially disturbed area is peculiar. The general form is egg-shaped, the egg-shaped portion being on the side directly exposed to pressure. The axes of the structure trend very rapidly over small areas.

The repetition of "dual deposits" already mentioned in Class B is also to be seen in Class A associated with the iceward side of the *roche-moutonnée*. This appears in the "Zone of Anticlines" of the Møen area, as will be shown later.

#### GENERAL APPLICATION OF THE PRINCIPLES OF GLACIAL TECTONICS TO THE MØEN SECTIONS.

The disturbances in Møen are local and only extend for a distance of about 3 miles south. This fact was pointed out by LYELL in 1837 (1).

The disturbances are superficial, the disturbed chalk being intimately associated with the overlying drift.

The structure agrees with the "*roche-moutonnée*" type of disturbance (Class A). It can be divided into two series of sections, north and south. In each of these areas there is definitely associated with a "core," or nucleus of the structure:

To the south the central unit of structure is the Dronningestol.

To the north the central unit is the coast area known as Slotsgavlene.

Between the two is a drift-filled central basin called Sandskredsfald and Avlegaardsfald.

The structure as shown by thrust-planes is developed on the iceward sides of both of the sections. On the north thrust-planes are well developed in the Taleren, to the south thrust-planes between a series of huge anticlines on the iceward side of the Dronningestol. The angles of inclination of the thrust-planes have a definite gradation when the latter





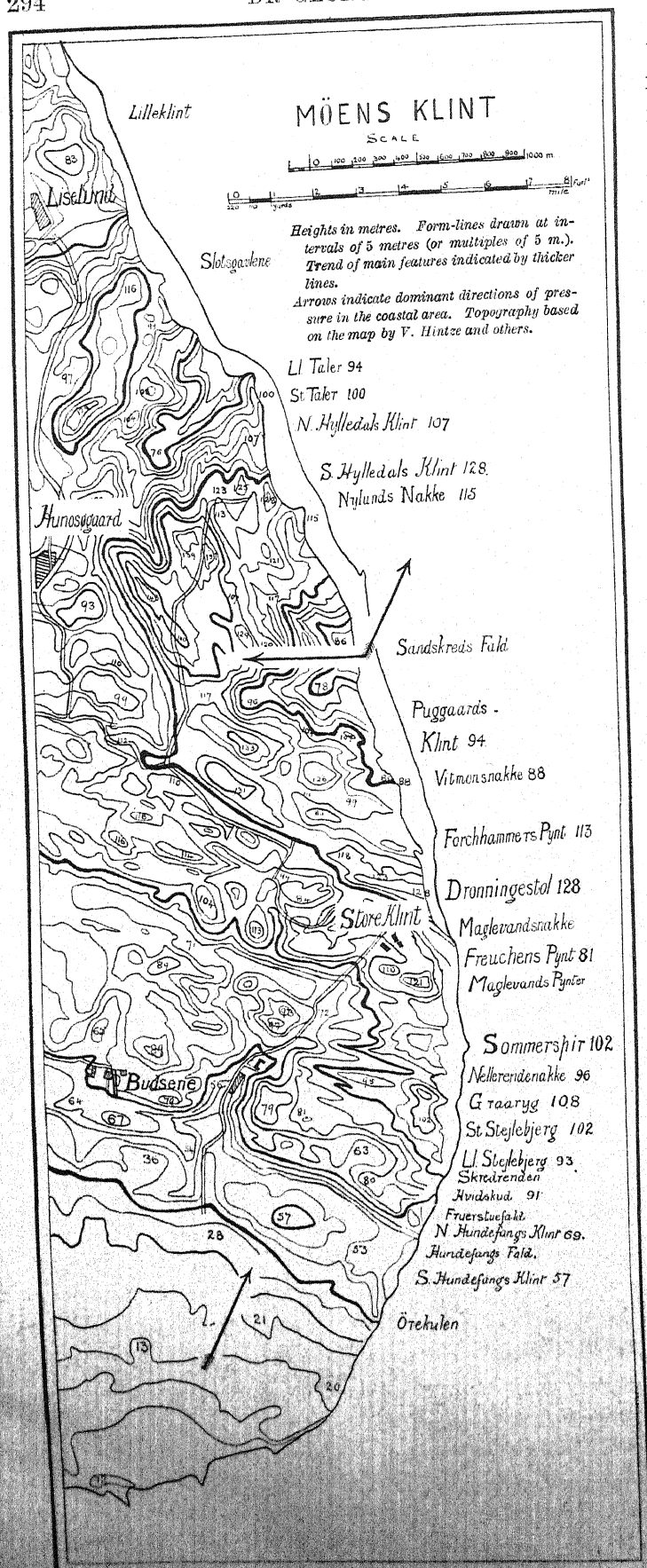


FIG. 2.

texture. In places it is brecciated, rubbly, marly, shattered, slicken-sided, in others homogeneous.

4. The bedding in places is so extremely fine as to suggest rearranged chalk paste, or pipeclay (fig. 3).

5. The larger curves in the chalk are all of the same type, resembling the distortion of the fundamental "flow-form" of viscous bodies (fig. 1).

6. True tectonic folds on a small scale occur usually in the lower parts of the sections.

7. Faults of three types occur:

- (a) Large faults due to the settling down of the deposits.
- (b) Smaller faults associated with small tectonic folds.
- (c) Fault-like fissures on the leeward side of Dronningestol. Other fissures occurring inland have been described by PUGGAARD.

8. Much of the chalk is outlined above and below by drift, and these isolated masses of moulded chalk simulate in general appearance chalk erratics, the internal structure suggesting differential movements of the constituent layers of chalk.

9. *Palæontology*.—The apparent rarity of fossils, with the exception of broken pieces of belemnites, is noteworthy. The chalk was ascribed by BONNEY to the zone of *Belemnitella mucronata*, but is now believed to be *Maestrichtian*. ? *Ostrea* (*Gryphæa*) *vesiculosus* was found and identified for me by Mr V. HINTZE. A specimen of a terebratulid was obtained from the chalk near the base of the cliffs, at the southern end of the Dronningestol. Lying on the ground close to this terebratulid was an almost perfect specimen of *B. mucronata*. This may have been

derived from chalk higher up the cliff, but cannot have travelled far from where it dropped. According to Dr SAHNI this terebratulid is *Chatwinothyris* (*Terebratula*) *lens*, and its presence is of considerable interest; it suggests the derivation of the chalk from different horizons of the undisturbed outcrop, for *T. lens* is of Danian age, whereas *B. mucronata* is confined to lower beds.

(b) *The Drift.*

Sections in the drift are invariably obscured by slips. This material occurs as a rule in narrow V-shaped ravines especially in the south. The central area consists largely of drift, filling a chalk basin.

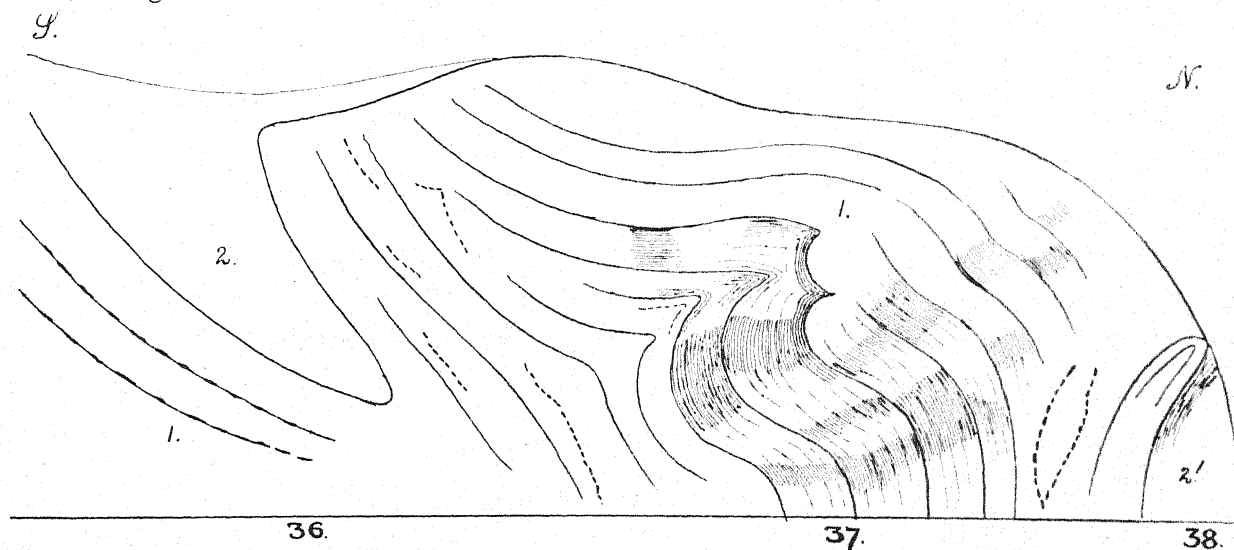


FIG. 3.—Gukkenchulefald.

1. Extremely fine-bedded chalk. 2 and 2'. Dark grey stoneless drift clay. High steep-sided wooded ravine above the section at 2. Height of section about 20 feet.

The succession of drift to the south near the lighthouse is as follows (5, pp. 390-1):—

5. Stratified sands and gravel with occasionally large erratic blocks 40-100 feet.
4. Unstratified yellow sandy clay, with pebbles and angular Scandinavian \* erratics. 40 feet.
3. Unstratified blue clay or till, small pebbles and fragments of Scandinavian \* rocks. 20 feet.
2. Stratified loam and sand with shells. 5 feet.
1. Chalk with a breccia of broken chalk flints.

The same succession of drift is marked by PUGGAARD as reappearing in the V-shaped ravines notably in the south, the order of arrangement being transgressed by thrust-planes in only a few cases.

Mr HINTZE, on the other hand, regards the succession of drift in the narrow drift-filled ravines in the south, and I believe elsewhere, to consist of two boulder clays with intercalated clay and sand, these beds apparently corresponding to Nos. 3 and 4 above.

This interpretation of the succession is as follows:—

5. Chalk with rubble and breccia thrust-plane.

\* Erratics are also very plentiful in the Island of Rügen, many of which have been derived from East Sweden and Mid-Baltic Islands.



4. Upper boulder clay, sandy in most cases with brown flints.
3. Marine clay and sand from the interglacial.
2. Lower boulder clay. Dark grey stoneless clay with little flint (=blue clay, No. 3 of PUGGAARD).
1. Chalk.

The position of the thrust-plane relative to the beds is always the same. I regret to say that owing to the extensive slips I was only able to insert the drift in the form of two lithological series in my sections. BONNEY also regarded the drift in the cliffs as of two series.

Clear evidence of the nip-in of the drift at the bottom of a V-shaped ravine was seen in the southern section (see fig. 1, No. 9, for example).

It is quite clear from the sections that the drift primarily associated with the disturbed chalk consists chiefly of the lower boulder clay associated with sand, whilst later glacial deposits fill in the ravines and basins.

In most cases there was great difficulty in differentiating what might be marine clay (3) from lower boulder clay (2), and Mr HINTZE also experienced the same difficulty in the special cases to which I drew his attention.

In view of the evidence of the thrust-planes given in this paper, notably in the southern part of the area, one can appreciate and explain the evidence set out by BONNEY on p. 323 of his paper, which is as follows:—

"We sometimes had the opportunity of examining from the beach a continuous wall of chalk beneath one of the apparently infolded or unfaulted masses of drift, and we were unable to detect in it the slightest sign of rupture or displacement."

The upper surface of the included boulder clay has acted as a lubricated glide-plane, and this plane clearly transgresses drifts of various levels in some of the sections. This drift shows signs of pressure and has been planed off into wedge-shaped masses in zones of great pressure (see fig. 1, Nos. 8, 9, and 12).

(ii) *Sections in the Northern Part of Møens Klint. Slotsgravlene and the Taleren.*

(a) *The Slotsgravlene "Core."*

The section described as the Slotsgravlene "core" is the lower part of the chalk of that area numbered 63 to 67 in the sections of PUGGAARD, 1851 (3). Here the chalk is much brecciated in the lower part, and this crushed chalk is overlain on the southern side by gently dipping chalk associated with bands of flints, this again being overlain by glacial clays and sands mostly masked by talus.

Taken as a whole, the "core" bears a striking resemblance to the disturbed chalk at Royston, Hertfordshire, in England. Traced northwards, the chalk begins to dip to the north and is finally replaced by a covering mantle of drift. The important feature lies in the low angle of the drift-covered surface of the chalk, which marks a thrust-plane, this angle being in striking contrast to the almost vertical thrust-planes of the Taleren.

The absence of detailed evidence in the cliffs between the "core" and the Taleren is explained on the view that the apparent talus-slope is really the strike of a thrust-plane in solid chalk, due to a pressure from the east. The deceptive appearance of apparent talus-slopes was referred to by LYELL, 1837. The north-south trend of a marked slope of chalk or drift-covered chalk dipping seawards is one of the chief features of the northern sections, this slope being associated with pronounced thrust-planes.

(b) *The Geological Structure of the Taleren.*

The remarkable sections of the picturesque bluffs known as the Taleren have always been an object of interest to geologists (3, PUGGAARD's section, Nos. 54 to 59).

The coast-sections between Nos. 54 to 59 may be regarded as a zone of thrust-planes, the chief characteristics of which are as follows:—

1. Movement in two directions, *i.e.*, one approximately parallel to the coast, and the other in a direction at right angles to the coast.
2. The presence of well-marked thrust-planes between the chalk and intercalated drift, the thrust-planes having a high inclination, much greater than the one described at Slots-gavlene. Other intercalations of drift are shown in the section of Store Taler, and these show a lower angle of inclination.

The V-shaped notches in the chalk occupied by the drift exhibit sections at right angles to the coast-section, and these sections have often been figured. The relationship of the chalk to the drift along the steeply inclined thrust-planes is clearly shown. The significance of the curves developed in the chalk of Store Taler lies in their exhibition of the asymmetrical curve characteristic of flow-movement, and suggests differential movement of individual layers of chalk. A comparison of both lines of sections proves that the chalk forming Store and Lille Taler is a mere shell of chalk lying on a bank of drift, and that the strike of the latter is approximately in a direction parallel to the coast, hence dominant pressure at this point has been towards the west.

This line of strike coincides roughly with the apparent talus-slope of Slotsgavlene. Reviewing the evidence as a whole, we appear to have the following connected sequence of events. The formation of the Slotsgavlene "core," and the heaping up of masses of chalk and drift on the iceward limb of that "core," ultimately leading to the production of what may be described as the Taleren-horst with the progressive rise in dip of the thrust-planes. Against this horst the subsequently formed beds of chalk have been "folded," and this is shown in the curves developed in the Nylandsnakke Bluff (Nos. 49, 50). The gentle dip of the chalk overlain by drift towards the ravine (48) limits the area of dominant disturbance in the north, and supports the view that the structure in this part of Møens Klint forms an independent unit with its own sequence of events.

The relationship of the chalk to the drift in this ravine adjoining Nylandsnakke is obscure.

The general principles of structure associated with the Slotsgavlene "core" are clearly shown in PUGGAARD's section, 1851.

(iii) *Sections in the Southern Part of Møens Klint.*(a) *The Dronningestol "Massif" (Nos. 26 to 34 of PUGGAARD's section).*

The chief characteristics of the Dronningestol "Massif" are as follows:—

1. The bluff has a specialised structure. It is composed of an aggregate of individual masses of disturbed chalk, each associated with thin strips of drift.
2. The chalk forming the northern and southern limbs of the "massif" dips in opposite directions.
3. The southern or iceward side of the "massif" is flanked by beds displaying signs of great pressure.

4. The leeward or protected flank suggests sliding and faulting.
5. Transverse sections and the downward slope of the Dronningestol bluff inland suggest that the structure has the form of an elongated dome.

The beautiful detailed structure shown by PUGGAARD (3, section Nos. 26-36) was only seen by me in the cliffs adjoining the seashore, but this structure fits in with PUGGAARD's structure (5, p. 392, fig. 52).

Regarded as an important unit of structure the "massif" is a "core," but of a type unlike that of the Slotsgavlene, the nucleus in this case being composed of squeezed, folded, and faulted chalk, and not a brecciated outcrop. The enquiry then arises as to whether such a "core" exists and is hidden by later-moulded chalk. The view that the "core" in this place is composed of intensely squeezed chalk appears nearest the truth and the one most capable of demonstration. That such "cores" have been formed by ice has already been shown by me in the case of the contorted London clay of the disturbed deposits of Messrs Bolton & Co.'s brickyard, Ipswich (18, 22).

The exceptionally large structure forming the Dronningestol is a "massif," which has obviously acted as a horst to the subsequently formed, squeezed zone of anticlines to the south. The portion of the cliffs between the Sommerspir, which marks the northern limit of the best-developed anticlines, and the southern flank of the Donningestol is now largely obscure except in the lower part near the shore-line. This portion, as shown in PUGGAARD's section (Nos. 20-26) shows a development of faulted folds and crushed chalk, and the upward extension of this structure is also shown in PUGGAARD's section.

That the portion of the cliffs between Sommerspir and Dronningestol has been subjected to exceptional pressure cannot therefore be doubted. The arrangement of the drift relative to the chalk in a section at right angles to the direction of the shore-line at Freuchens Pynt appears to be a drift-filled shallow basin of chalk sloping towards the sea.

(b) *The Zone of Anticlines and Thrust-planes* (fig. 1).

To the south of the area, between Hundefangs Klint and Sommerspir, there is a remarkable development of seven anticlines separated from each other by thrust-planes associated with drift deposits in V-shaped clefts, partly shown in fig. 1. The relative sizes of those anticlines do not vary greatly, but they show a general squeezing-in when traced from south to north. Measured from the central axis of a fold to the periphery the general thickness of the beds in each is almost 200 feet. *The boulder clay on the north side of each of the V-shaped clefts is always lower boulder clay resting apparently evenly on the chalk, whereas on the other hand the southern side of the clefts is always marked by a well-developed thrust-plane.* There is also good evidence for a pinching-in of the drift towards the lower parts of the clefts. Some of the thrust-planes have been inserted by PUGGAARD, others apparently not visible in 1851 are well displayed at the present time. Sommerspir marks the commencement of the breaking-up of the anticlines; it also marks the point of a slight change in the direction of thrust, as shown in the strike of the chalk below sea-level. The remarkable structure of the compressed zone of anticlines raises a most important point in structure. It has already been noted that the relative position of the lower boulder clay and chalk on the northern sides of the narrow ravines is always the same, whereas the southern side is bounded by a thrust-plane.

PUGGAARD's section, which shows in places a regular lining of drifts as concentric V-shaped layers, is not confirmed in these particular sections. The repetition of structure and the repetition of the same drift material in the same relative position can only be explained by



ice-movement as follows. Thick layers of chalky englacial material with drift above were gradually inclined owing to obstruction to movement. The curves and structure assumed are well shown in PUGGAARD's drawing of Dronningestol.

Eventually a fracture occurred and took the form of a curved thrust-plane; the upper surface of the drift flanking the curve formed a suitable plane of movement. This process was repeated seven times. The angles of inclination of the thrust-planes decrease towards the south and the anticlines also become less developed.

The crushed anticlines are therefore distorted flow-overfolds. The ravines with drift are therefore not complementary troughs to anticlines, and hence the structures are not true folds.

The commencement of this zone is shown in fig. 1.

The peculiar forms assumed by the curves in the various chalk overfolds are paralleled in the forms assumed by ice under pressure, and similar forms have already been recorded in the Mud Butte Area of Alberta, Canada (24).

Hence the development of such forms, so unlike ordinary tectonic structure, could only be possible if the chalk involved were in the form of comparatively thin intercalated lenticles. These lenticles have become recemented by chalk paste. Further proofs of this view, however, will be given when dealing with the structure on the leeward side of the Dronningestol "massif." I believe that the Cromer coast-sections afford a complete confirmation of this view.

The gradual variation of and decrease in the angles of inclination of the thrust-planes from Sommerspir southwards follows as a natural result of the variations in the amount of pressure.

The zone of the seven anticlines is obviously the last stage in the structure. There has been little or no transportation of the crest of one anticline over that of the one immediately to the north of it. On the other hand the Dronningestol "massif" shows clearly that such transportation has occurred from the iceward to the leeward side. Where then was the source of origin of these chalk masses? They can only have been derived from the compressed zone between the Sommerspir and the Dronningestol, but prior to the formation of the zone of anticlines. The form of the individual masses of chalk bounded by drift as shown in PUGGAARD's section indicates that these masses are portions of folded chalk only, and the broken structure in the area mentioned suggests this as the source of origin; this crushed zone really formed the buttress against which the later chalk was compressed, whilst Sommerspir formed the sigmoid curve of this mass. This view also explains the difficulty of the arrangement of the drift on the iceward flank of the Dronningestol, and also the change of strike of the chalk at Sommerspir. It also supports the view that this part is of great structural importance.

Traced inland, all the chalk-bluffs of this area decrease in size and apparently the ravines narrow seawards and widen inland, reminding one of the pinched-in zones in the Ipswich (Hadleigh Road) Area, and the development of elongated domes and spoon-shaped basins.

(c) *The Structure of the Leeward Side of the Dronningestol* (see PUGGAARD's section, Nos. 34-44).

The chalk and drift which show a definite connection with the structure of the Dronningestol extend for a much smaller distance on the leeward side than that on the iceward or northern side. These beds show well-marked characteristics:

1. They dip downwards to the south (approximately), and also increasingly rise westwards when traced towards the north.

2. The angles of dip decrease progressively when traced from south to north.
3. The amount of drift increases away from the Dronningestol; and the disturbances decrease in amount also towards the central basin.

The structure drawn in 1925 differs somewhat from that of 1851, for I saw no sign of the faulted faces of chalk (Nos. 40, 43, 44). The large curve of PUGGAARD (No. 37) was only partly exposed this year and reminded me of the extremely small curve of similar form seen in the section at Claydon Chalk Pit, Suffolk (22).

This section, fig. 3, on the immediate flank of Dronningestol adjoining FORCHHAMMER's Pynt deserves special mention (Nos. 36, 37, 38 Gukkenchulefald, and Plate I). There we have a section of about the average thickness of the overfolds already mentioned, bounded north and south by drift. At spot 36 the drift is tongue-shaped near the shore, at spot 38 the drift is slightly arched over and forms part of that filling an almost vertical cleft. This section therefore forms the base of the diapire curve just mentioned, and the drift is shown in detail by PUGGAARD.

The very beautiful structure shown by the finely banded chalk (fig. 3) is unlike that seen by me in any other part of the cliffs and suggests a remoulding of chalk paste, and the type of downward-flow movement illustrated experimentally by Professor W. J. SOLLAS (12) and E. C. CASE (11). The tendency seen in the Ipswich (railway line) sections (23), for masses of Crag to become gradually isolated into moulded individual lenticles on the leeward side of the "core," suggests that there has been the same tendency in the chalk of this area. Such masses may reasonably be associated with "faults." The Ipswich sections also show the breaking-up into drawn-out lenticles of such masses under the influence of pressure, when approaching the iceward side of the next "core." The masses of chalk forming the Taleren were probably deposited at the same period as the initial stages of the formation of the Dronningestol "massif." The ice-theory would explain "faulting" on the leeward side as being due to crevasses. Other faults are obviously due to cracks, due to the settling-down of the masses of chalk.

## VI. DIRECTIONS OF PRESSURE AND MOVEMENT.

The topography of the map (fig. 2) is very suggestive, but as this paper only deals with the coast-sections, the discussion of many of the most interesting points in the general area must perforce be omitted.

The following are the chief features which have special reference to the coast-sections:—

1. The west-north-west-east-south-east trend of the higher ground (chalk) of the zone of anticlines in the south.
2. The north-east-south-west trend of the higher ground (chalk) in the Slotsgavlène or northern area.
3. The elongation of the topographic features of the high ground north of the central basin and south of the Taleren, the main direction being approximately north-north-west and south-south-east or approximately at right angles to the direction of (2).

### *Pressure Directions* (map, fig. 2).

Directions of pressure, derived from the geological structure are as follows:—

1. In the south the dominant pressure was approximately towards the north-east.
2. In the north the dominant pressure was towards the west, the lesser pressure being towards the north-east.

Applying the principles of movement in relationship to pressure, derived from the Hadleigh Road (Ipswich) deposits, the directions of movement are as follows:—

1. In the south, movement was towards the north-east, and the axes of the anticlines on the iceward side of the Dronningestol are therefore at right angles to that direction.

2. In the north, the direction of movement was in the same direction as the resultant of the two pressures. These pressures progressively varied northward, the one to the west increasing, the other decreasing in that direction. The general strike of the disturbed beds therefore occurs in two directions:

- (a) In the tensional area of the central basin it is along the line of the resultant.
- (b) In the pressure-zone associated with the iceward side of the Slotsgavlène "core," the strike of the beds is at right angles to the resultant.

The combined effects of these movements was the production of a horse-shoe type of topography and a pivotal motion, the fulcrum of which was on an axis which passed through the central basin.

Incidentally the principles of movement described appear also to account for the topographical facts already mentioned, but not dealt with in detail.

## VII. SUMMARY.

1. The disturbed deposits of Møens Klint are entirely due to glacial action, but on a very unusual scale. They bear no relationship to earth-movements.

2. There are two centres of disturbance, one to the north, the other to the south, each associated with definite structure.

3. The whole of the chalk has been transported, with perhaps the single exception of the Slotsgavlène "core," which appears to be a brecciated outcrop of fine chalk uncontaminated by drift. The Dronningestol "core" appears to have a nucleus of broken and folded chalk.

4. The building-up of the structure over the northern (Slotsgavlène) "core" was completed about the same time as the construction of the Dronningestol "massif." This latter structure finally prevented any further passage of chalk over its crest.

5. The zone of anticlines was built up last of all, and was followed by a final phase in which the dominant products were boulder clay and sands and gravels; this material subsequently filled in the central basin and any other inequalities of the surface and formed minor features in the general topography.

6. The principles of structure enunciated from previously studied glacial sections are applicable to the Møen area, where the structure, however, is on an unusual scale.

7. The additional evidences obtained from Møens Klint is primarily concerned with the zone of anticlines. There are seven anticlines as well as portions of others destroyed, whereas in the Ipswich area there is only one, on the iceward side of the main sigmoid curve. All the seven anticlines have been moulded from ice overloaded with englacial (chalky) material surmounted by englacial drift.

This evidence forms the "coping-stone" for the view that this type of tectonics is entirely associated with ice-action and fundamentally different from ordinary earth-movements due to lateral pressure.

Finally, it should be said that a certain amount of evidence is lacking in the Møen area as to the structure associated with the initial and final stages of the disturbances. This evidence is to be seen in the Lønstrup sections, and will be described in the succeeding paper.



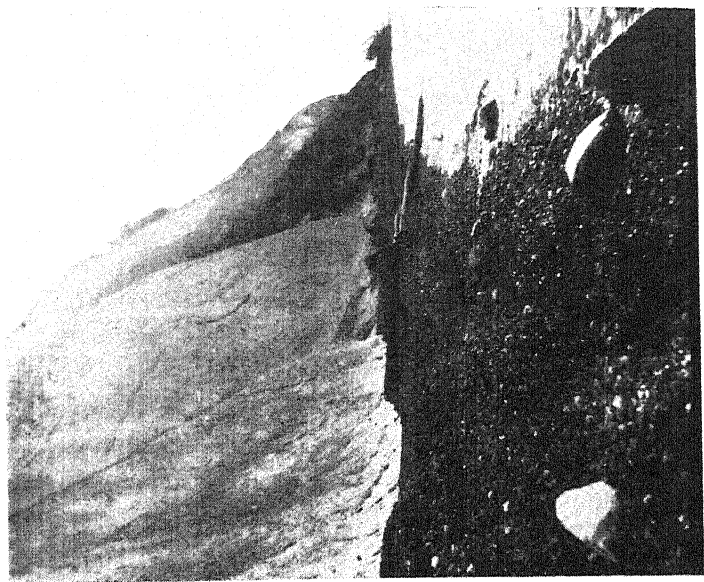
In conclusion I beg to thank the authorities of the University of London for the award of a grant from the Dixon Fund for the purpose of defraying the expenses of this and the Lønstrup investigations. To Dr VICTOR MADSEN, Director of the Danish Geological Survey, I am under many obligations for which I express my gratitude. To Mr V. HINTZE I am also indebted in many ways and am especially grateful to him for the extremely kind way in which he placed his great experience of the geology of Møens Klint fully and ungrudgingly at my service. To Mrs ELLEN MERTZ of the Danish Geological Survey I am also grateful, and thank her especially for the help she afforded owing to her excellent knowledge of the English language.

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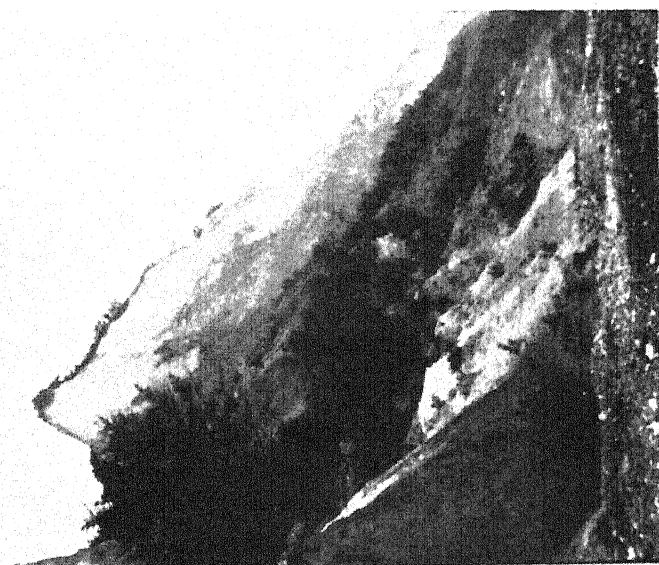
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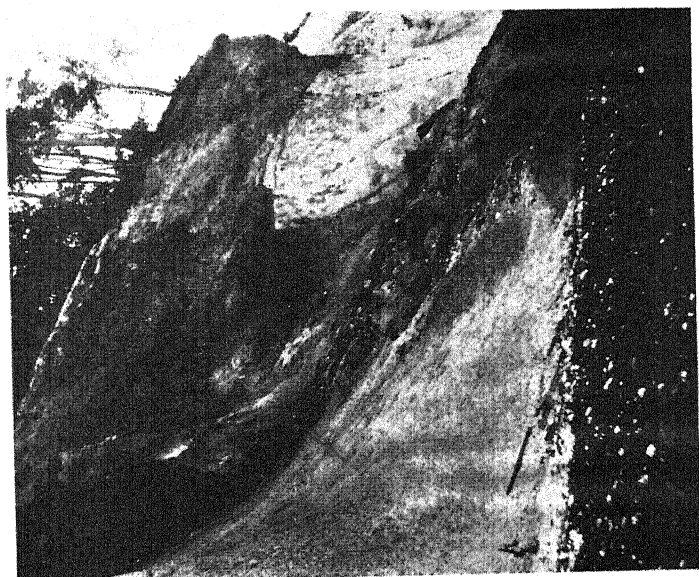
Dr GEORGE SLATER on "The Structure of the Disturbed Deposits of Moens Klint, Denmark."—PLATE I.



C.  
[No. 37 of Fig. 3.]



Vitmonsukke and slips of drift.



B.

[No. 36 of Fig. 3.]



A.

Photo, G. Slater.]

GUKENCHULEFELD.  
(SHORE SECTIONS.)



[No. 38 of Fig. 3.]  
Gukenchulefeld to left. Vitmonsukke to right. Clay drift  
in foreground.





XIII.—The Disturbed Glacial Deposits in the Neighbourhood of Lønstrup, near Hjørring, North Denmark.\* By George Slater, D.Sc., D.I.C., A.R.C.S., Imperial College of Science and Technology, London. *Communicated* by Dr G. W. TYRRELL. (With Two Plates.)

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I. INTRODUCTION.

Lønstrup is a small fishing village and summer resort, situated on the west coast of North Jutland, a few miles west of Hjørring in the district known as Vendsyssel. The country generally is low and treeless, but is noted for its comprehensive schemes of land reclamation, and the scientific development of its agriculture.

In the neighbourhood of Lønstrup the monotony of the country is relieved by two low hills, the one, a little inland, is known as Vennebjerg, the other, known as Rubjerg Knude, lies some 2 miles to the south-west and is dissected by the coast-line, the apex of the hill being marked by a lighthouse. These two adjacent hills formed islands in the Yoldia Sea.

The coast-line has a uniform north-east, south-west trend, and cliffs occur from Lønstrup to Lokken in the south-west, a distance of between 7 or 8 miles, the cliff-scenery being generally similar to that of the Norfolk coast near Cromer.

The stretch of coast characterised by disturbances of a particular type only extends from Det lille Blaa (near Lønstrup) to Stensnoes in the south-west, a distance of  $2\frac{1}{2}$  miles, and it is this strip of coast which forms the subject-matter of the present paper. The centre of this portion of the cliffs and the highest ground is marked by the lighthouse, hence these cliffs are more correctly described as the Rubjerg Knude Cliffs. The height of the hill is considerably increased by an accumulation of blown sand which unfortunately masks the surface geology. Unlike many other cliffs, there are no important indentations or buildings on the summit, and but few marked topographical features, rendering the identification of particular portions of the cliffs a matter of some difficulty.

A few of the more striking features of the Rubjerg Knude cliffs are as follows:—

1. The hill has been dissected by the sea along a median longitudinal line.
2. The section shows the whole of the disturbed zone, and the initiation, development, and termination of disturbances of a particular type.

\* Part 9 of Thesis approved for the Degree of Doctor of Science in the University of London.  
TRANS. ROY. SOC. EDIN., VOL. LV, PART II (NO. 13).

3. All the disturbed deposits have a uniform direction of dip, which is approximately to the north-east, or north-north-east.
4. The section is at right angles to the general strike, hence there are few serious landslips.
5. The disturbed deposits consist entirely of glacial clays and sands.

## II. LITERATURE.

The literature dealing with these sections is comparatively small:

1. F. JOHNSTRUP in 1882 published a comprehensive work on the geological conditions in the northern part of Vendsyssel (1).
2. In 1899 the Danish Geological Survey published a short account of the sections, illustrated by a small plate of sections (2).
3. In 1916 State-Geologist AXEL JESSEN published a preliminary account on the dislocations in Lønstrup Klint, illustrated by a few photographs and one diagrammatic sketch (3). This paper also contains a useful summary of the history of the investigation of disturbed deposits in Denmark, a résumé of which will be given.

Unlike the Cromer area, the Lønstrup district has not yet been the subject of a special memoir by the Danish Geological Survey, and this may account for the general, if not entire, neglect of the sections in British glacial literature. This is to be regretted, as they have an important bearing on the question of the glacial conditions of the North Sea during Pleistocene times. This is a subject on which there has been much speculation, the evidence in support of the various theories having been derived almost entirely from the study of British coastal drift-deposits.

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## III. RÉSUMÉ OF THE HISTORY OF THE INVESTIGATION OF DISTURBED DRIFT-DEPOSITS IN DENMARK.

(a) F. JOHNSTRUP in 1882 (1) was a keen believer in the ice-theory, and attributed the disturbances to the horizontal pressure of the Scandinavian ice. A few of his conclusions are as follows:—

1. The dislocations are superficial, and are entirely a surface phenomenon of ice.
2. The uniform direction of dip is in accordance with the direction of movement of the ice-sheet.

3. The isolated and inclined clay layers were formerly joined together in the undisturbed areas.
4. An apparent succession could be traced at Maarup Kirke and compared with that in the more disturbed portions of the cliffs.
5. Variations in the structure and angles of dip of the beds in various parts of the cliffs were noted.

These conclusions are eminently sound and can easily be verified in the sections accompanying the present paper or seen at present in the cliffs.

(b) A. JESSEN in 1899 (2) took exception to the ice-theory and attributed the disturbances to earth-movements in the form of huge slips. His main objection to the ice-theory appears to be that there is no sign of differential pressure. This statement, however, will be shown to be incorrect. JESSEN's theory also fails to account for the thrust-planes which are one of the commonest features of the sections.

(c) In 1916, Dr V. MADSEN, Director of the Danish Geological Survey, examined the sections of Ristinge Klint, which are of the same type as those near Lønstrup (4).

Dr MADSEN proved that the undersides of a "fatty clay" formed thrust-planes leading to the formation of a "fish-scale" structure due to the gliding of beds of different lithology the one over the other, the clay acting as a lubricating grease. This movement was proved to be superficial and led to the planing of portions of the beds into wedge-shaped masses. The direction of dips of the beds also agreed with that required by the movement of the ice, and hence Dr MADSEN came to the conclusion that the structure was due to ice- and not to earth-movements.

(d) In 1913-14 Dr V. MADSEN investigated the Røgle Klint. Here the same characteristics occurred as before, but with this difference, that "the bed-sequence at a single spot fell against each other." This apparently means the beds were faulted? In any case, it led to the view that the structure was due to earth-movements. With a view to obtaining further evidence on this point the next investigation was made.

(e) In 1915 Dr V. MADSEN and his colleagues investigated the Lønstrup sections, and a preliminary report was issued in 1916 under the authorship of A. JESSEN (3).

This preliminary report deals mainly with particular points of structure, and the conclusion arrived at as a result of this investigation may be translated as follows:—

"Without regarding the question as solved, we have obtained from our examination the definite impression that the dislocations in Lønstrup Klint cannot be due to ice-pressure."

Mr AXEL JESSEN, who accompanied me during a preliminary traverse of the cliffs, made it quite clear that there was still no settled opinion amongst Danish geologists as to the genesis of the structure.

The views of FORCHHAMMER and V. HINTZE on the theory of the structure of Møens Klint are omitted as they have already been mentioned in the previous paper.

The trend of Danish opinion attributing the disturbances to earth-movements appears to be due to the influence of certain German geologists who have examined the analogous disturbances in the Island of Rügen. It will be shown that this view of the genesis of the structure is illogical and untenable. The failure to appreciate the work of the American glaciologists in Greenland towards the close of the nineteenth century appears to me the chief reason for the lack of support of the ice-theory by some workers in Denmark during the last quarter of a century.



## IV. METHOD OF WORK.

The preliminary traverse convinced me that the only way to solve the difficulty was to draw the whole of the disturbed sections to a uniform scale. As already mentioned, the only previous work I used was the plate of sections published in 1899 (2), which shows portions only of the cliffs. These were utilised for obtaining the heights of the cliffs at various places. Elsewhere the heights of my sections are approximate, but as the variations in height are comparatively small the amount of error cannot be serious in the scale adopted. The whole of the cliffs were measured from Lønstrup Brook to near Yvonnet Rende. The portions of the cliffs, however, between Lønstrup Brook and Det lille Blaa, in the north, and between Stensnes and Yvonnet Rende in the south are not considered in this paper, as the sections submitted embrace all the important points of structure of the disturbed zone. These sections (Plate I), if placed end to end, give a complete representation of the disturbances. The numbering below the drawings enables easy reference to particular parts of the cliffs, whilst the detailed notes on the sections themselves render lengthy description unnecessary.

In this paper I have introduced theoretical considerations with the detailed descriptions of the sections. This course appeared advisable for several reasons:

1. It clarifies the description and enables the reader to obtain a ready grip of the structure.
2. The analogy between the structure and that seen in arrested glaciers can be clearly demonstrated.
3. It spares the reader from having to re-examine the sections in detail, as would be the case if the theoretical treatment had been reserved until the end of the paper.

## V. LITHOLOGY.

The beds in the disturbed zone belong to two lithological series—clay and sand.

(a) *The "Diluvial Clay."*—The clay is very fine in texture, pale grey in colour, and stoneless. In some parts of the cliffs it is homogeneous and imperfectly bedded, in others, the clay is beautifully bedded and intercalated with sand. I obtained a specimen of *Macoma* (or *Arcopagia*) at the point 3200 feet from Det lille Blaa (Plate I). As with the sand, there is proof of movement *en masse*, and elsewhere of differential movement within the mass.

(b) *The "Diluvial Sand."*—The sand is fine-grained and silky to the touch, and contains plant remains. The original water-bedding is often preserved, proving that the sand has been transported as a cake, but in certain parts of the cliffs this has been replaced by the development of secondary structures due to differential movement of the constituent layers in the sand, a phenomenon of great interest. It is very difficult, however, to determine where one type of bedding terminates and the other begins. The types of structures developed in ice under the influence of stress are very imperfectly known. The structures seen in the ice of Franz Josef glacier, New Zealand, for example, if preserved in sand, after the slow melting out of the interstitial ice, would delude almost any geologist into believing that it was simply false bedding. I have drawn the attention of geological friends to a similar structure in the fine-grained sands of the Cromer coast, and they unhesitatingly attributed the structure to water-action. The abnormal angle of gradient, however, appeared to me to favour the view that it was due to ice-action associated with the development of numerous thrust-planes of the type I have described in the imbricate structure of the Sven glacier of Spitsbergen (9).

On the other hand, the beautiful structures developed in the sands when associated with

major thrust-planes are obviously of secondary origin and due to ice-pressure on frozen masses, the structure being the result of tangential thrust.

The original ice-structures preserved in unconsolidated sands in America have been described by C. F. BERKEY and J. E. HYDE (7).

## VI. STRATIGRAPHICAL SUCCESSION.

The sand and clay are intimately associated with one another and form a "sand-clay" unit; a pair of such deposits is repeated again and again throughout the disturbed zone. An examination of the junctions of the beds shows that in a sand-clay unit, the sand rests conformably on the clay, but the upper surface of the sand is transgressed by the under surface of the succeeding "fatty-clay," the plane of junction being a thrust-plane. This relative order leads to the assumption that the disturbed beds forming a unit have been removed together as one "cake," transported, and often redeposited in their relatively original positions. Hence the original stratigraphical succession is as follows:—

2. "Diluvial" sand (above), or Glacial sands, with plant remains in places (L of Plate I).
1. "Diluvial" clay (below), or Glacial clay without stones (K of Plate I).

Unfortunately this cannot be completely verified in the undisturbed area owing to the removal of the upper part of the succession. The undisturbed outcrop of the diluvial clay occurs to the north between Det lille Blaa and Grotten Point, and the upper surface of the clay forms a long low curve, but there is no sign of any diluvial sand, the clay being overlain by later glacial deposits. Hence the assumption appears warranted that a portion of the upper clay together with the diluvial sand has been removed from this part, and redeposited farther to the south-south-west.

Other points in the stratigraphy may be summarised as follows:—

1. Recent borings prove that there is a considerable thickness of drift-deposits beneath the diluvial clay and below sea-level, and that these beds rest on the chalk.
2. The Ældre Yoldia clay (interglacial) has been exposed on the Lønstrup shore; this bed occurs immediately beneath the diluvial clay, and was formerly exposed at Det lille Blaa.
3. Flanking the disturbed deposits at each end of the disturbed zone are later glacial deposits consisting chiefly of sandy boulder clay with what I regard as glacio-fluvial sands and gravels.
4. Lying unconformably on the edges of the upturned disturbed beds, towards the north and south, are the Saxicava and Yoldia deposits. These deposits thin out towards the apex of the hill near the Rubjerg Knude Lighthouse, hence the statement that the hill was an island in a Yoldia sea.

## VII. DETAILED DESCRIPTION OF THE SECTIONS.

### (i) *Order of Description of the Sections.*

In describing the sections the order adopted will be to follow the structure from the south-south-west towards the north-north-east, that is in the reverse direction to that of the direction of the movement which caused the disturbances.

The distinctive type of structure developed in the disturbed zone ceases near Stensnoes in the south-south-west. More strictly speaking, the distinctive type referred to is replaced

by structures much less pronounced, including a development of low anticlines and synclines, suggesting domes and basins, in the district near Yvonnnet Rende.

Hence the description of the sections commences near the place marked as Martørv Bakker (at 12,600 feet).

The advantages of adopting the order of description above are twofold:

1. It enables the relationship between cause and effect to be clearly followed.
2. It is the only method of demonstrating the cumulative effects of directed, concentrated pressure.

(ii) *Section between Brede Rende and Stensnæs* (Plate I and II, figs. 1 and 2).

(a) *The Initiation of the Disturbances*.—The section at Martørv Bakker is the key to the whole of the structure of the disturbed zone to the north-east. Hence the description of the sections will commence at the point 12,600; the part of Plate I to the south-west (12,600–14,400) will be described later. At the point mentioned (12,600), Plate II, fig. 1, slightly inclined beds of clay and sand abruptly cease, and against the steep face is a deposit of pale-grey sandy boulder clay. With the exception of the dip of the beds of clay and sand the section recalls those described in the railway sections of the Hadleigh Road Area (6). There is no proof whatever of the fault suggested by Mr A. JESSEN. The abrupt termination of the clay-sand deposits also recalls that seen in the Mud Butte sections of Alberta (10). Still more significant, however, is the analogy of the structure with that seen in the dirt-filled ice forming the terminations of all the stagnant glaciers of Spitsbergen, Greenland, and New Zealand. The analogy is so close as to strongly suggest that the structure here seen is that of the stagnant end of an overloaded ice-sheet, in which the melting back of the glacier has been arrested, and the structure has been preserved by the blanketing of boulder clay. Hence the englacial layers have been preserved in their relatively original positions by the slow melting out of the interstitial ice.

I have shown in the case of the Nordenskiöld glacier of Spitsbergen that the melting of the ice face bears a direct relationship to the air-temperature, when unprotected (8 and 9). But ice faces smothered with debris are also common in glaciers all the world over.

Again in the Sven glacier I have shown that the stagnant end of a glacier acts as an obstruction to the movement of the ice over a considerable area, and induces the development of a beautiful series of thrust-planes; moreover, that these thrust-planes have various angles of inclination (9). Professor E. J. GARWOOD has also proved that this phenomenon is associated with the layers of englacial material in Spitsbergen (11, Plate xiii), and Professor T. C. CHAMBERLIN \* has illustrated the same point in the case of Greenland glaciers.

Now in these Danish sections we have exactly the same type of structure. For example, we may note the beautiful thrust-plane at spot 11,800, and the intense crumpling and contortion of the beds with which it is associated. This structure clearly demonstrates the passage of moving beds against and over an obstruction.

(b) *The Horst* (11,000–11,600).—Here we have a mass of clay intercalated with drawn-out lenticles of sand and associated with disturbed deposits, the iceward side of the clay forming the sigmoid curve.

This structure clearly points to greatly increased pressure. The question arises as to what has caused this banking of clay out of all proportion to the amount of sand. The answer is given by an examination of the section (9600–11,000). At spot 10,600 there is a packing

\* See Literature in paper on Møen.



of drawn-out and broken fragments of clay in a matrix of sand, whilst farther to the north-east sand predominates but is associated with drawn-out layers of clay.

The explanation is simple. The whole consisted of interbedded bands of clay and sand in the form of englacial layers experiencing differential movement. The clay from its nature moved easily, the sand with difficulty, and in consequence the clay was drawn out and concentrated more and more to form the mass which ultimately became the banked-up and immobile horst.

The horst therefore marks a zone of directed and concentrated pressure. Some of the material flanking the north-eastern face of the horst must have passed over the crest prior to the deposition of the boulder clay at 12,600, but the stagnant end, judging from the structure, could only have been melted back a few hundred feet, before being protected by its mantle of boulder clay. Such a view would account for the material deposited at Stensnæs. The absence of thrust-planes indicates a lessening of pressure towards the end of this section, in the neighbourhood of Brede Rende.

It has already been mentioned that in certain parts of the disturbed area the order of superposition of the units of "clay and sand" could be clearly seen. It is noteworthy that in this portion of Plate I all such relationship has been destroyed. Deposits which have elsewhere apparently moved as a whole have here been drawn out and separated, as a result of moving differentially in the form of individual layers.

Before leaving this part of the area, reference may again be made to the sigmoid curve of the horst. The direction of the included lenticles proves an upward motion in the region of the curve, and recalls the sections near Ipswich where the initiation of the sigmoid curve and its development were considered.

(c) *The Stensnæs Deposits*.—(Plate II and Plate I, at 14,000). These deposits may be divided into two series:

2. Gravel and sand.
1. Contorted loamy leaf-bearing sands.

*The Gravel and Sand*.—This deposit is of interest as it is a typical water-sorted gravel of morainic type intimately associated with the overlying deposit of boulder clay. Fragments of shells are common, some of these on the talus-slope being identified by Professor A. M. DAVIES as *Astarte* sp. and *Macoma* sp.

*Loamy Sands*.—It has already been suggested that these are transported deposits and prior to the deposit of gravel and boulder clay.

They are chiefly remarkable for the contortions developed. These are regarded by Mr A. JESSEN as undoubtedly caused by ice.

For some time, however, I was prepared to ascribe the contortions to the slipping of the loamy material down an incline during the settling down of the mass. J. G. GOODCHILD over fifty years ago drew attention to contortions in glacial clays apparently due to such movement (5). The contortions at Stensnæs, however, are similar to those developed in the supposed Varve clays of New South Wales of Carboniferous age.

It is noteworthy that the Stensnæs deposits are deposited on the leeward side of the thrust-zone, and hence were subjected to tensional action during a downward movement, and pressure phenomena when being carried up the inclined plane where they now rest. Such movements would be sufficient to contort the beds, and would also explain the peculiarity in type of the contortions. Some amount of slipping during settlement must also have occurred.

(iii) *Section between Rubjerg Knude Fyr and Brede Rende (Plate I).*

(a) *The Zone of Thrust-planes.*—The type of structure seen at Brede Rende in Plate I continues up to the point 8800. From this point to the north-eastern end, that is up to Rubjerg Knude, the beds have definite characteristics which are repeatedly reproduced. The chief features of the structure are as follows:—

1. This section of the cliffs may be described as a zone of thrust-planes.
2. The larger thrust-planes have a gradually increasing angle of inclination when traced towards the north-east.
3. The succession between the clay and sand may be traced between Søndre Stenstue Rende 7600 to Rubjerg Knude Fyr 4900.
4. Beautifully bedded clays occur at four places and at approximately equal distances (see spots 7900, 6900, 5900, 4900).
5. The isolated slabs of clay are of about equal sizes in several cases.
6. The structure in the zone of thrust-planes begins with the formation of a horst associated with the finest thrust-plane in the area (see spot 8200), and this horst has a sigmoid curve at 7600 in the cliffs called Søndre Stenstue Rende, recalling some of the points of structure near Martørv Bakker in Plate I.
7. At 8400 there is a thrust-plane in the sand, suggesting the entire squeezing out or removal of the intercalated clay (seen at spots 8400–8600).
8. There is a localised development of structure between 7200 and 7600, that is, against the iceward side of the sigmoid curve at Søndre Stenstue Rende.
9. The upper limits of the isolated slabs of clay generally possess a wedge-shape, due to the shaving off of the upper part of the clay during movement and to friction below.
10. The thrust-planes are marked by straight lines in order to show the general angle of dip. They all partake of the form of a sigmoid curve, however, the curve flattening above and below, recalling the form of the thrust-planes in the Mud Butte Area (10).
11. Some of the clay masses show foliated structure characteristic of differential movement (see spots 6550, 6200, 5400, 5100, 4900).
12. The bedding of the sand beneath the thrust-planes may be either transgressed (as at spot 6300), or the sands may be generally contorted (5700–5800) or the upper part only of the sand disturbed (5300).

(b) *Theoretical Suggestions and Considerations.*—The greater development of the sand to the S.W. in the Brede Rende area, even after taking into consideration the leaching process already described in Plate I, coupled with the absence of a stratigraphical succession, can be readily understood on the theory that the earlier stages of ice-erosion took place in the diluvial sand. As portions of the sand were removed, the later stages of ice-erosion involved the incorporation of the basal layers of the diluvial sand, with the upper portion of the underlying diluvial clay. This recalls and is suggested by the fact that such action occurs and has been described for the Crag and London clay in the Ipswich Area.\* Hence the structure shows repeated inversion of the succession, due to tangential thrust.

The isolated masses of clay and sand may be regarded as having been all derived from the same horizon approximately, sheets of transported material having been subsequently divided

\* See Literature in paper on Møen.

up into the numerous isolated and inclined masses now seen in the cliffs, dissected by thrust-planes.

(iv) *Section between Maarup Kirke and Rubjerg Knude Fyr* (Plate I).

*The Zone of Compressed Anticlines and the Stortorn Subsidiary Horst.*—The section (Plate I) shows the most complicated structure in the whole of the disturbed zone, and I am extremely glad that I visited the Møens Klint area before examining the Lønstrup sections, as the former (zone of anticlines) gives the clue to the latter. The main points of structure may be summarised as follows:—

1. A horst occurs to the south-west, composed of flow-overfolds in clay and associated with thrust-planes (4400–4800).
2. The increase in the amount of dip of the thrust-planes continues and culminates in an almost vertical face (sigmoid curve at 4300). This point divides the zone of compressed anticlines from the zone of thrust-planes. The structure of the horst reminds one of that seen on the iceward side of the Dronningestol massif of Møens Klint.
3. From the point 4300 to the north-east end of Plate I (Maarup Kirke) the angles of inclination of the thrust-planes gradually decrease.
4. From 1300 to Maarup Kirke, the structure resembles that of the zone of thrust-planes (Plate I).
5. The zone of compressed anticlines is best developed between 1400–3500. In this section there are four anticlines, each containing a central core, these are: 1400–1600, 2100–2400, 2600–2900, and 3000–3400.
6. The junction between the clay and sand at spot 2400 is noteworthy. Here the line of thrust occurs between the upper surface of the clay and the sand above, that is, in the reverse position to the normal one, and therefore produced from an anticlinal structure (see dotted lines) of the flow-overfold type.
7. The thicknesses of the sand on either side of a squeezed clay core correspond closely, cf. spots 2700 and 2900, and 2100 and 2400.
8. The amount of compression decreases towards the north-east. At 1500 the core of the anticline is peculiar, and not at all like part of a tectonic fold. The structure is due to flow-movement, and this accounts for the change in character of the clay above on the two limbs, the one on the exposed side (1400) being compressed and showing wavy bedding, the other limb on the leeward side being composed of opened-out layers of clay and sand of a peculiar shape and structure.
9. The Stortorn mass of clay formed a subsidiary horst against which the beds in the zone of anticlines were compressed. In general structure it is not unlike the horst at Søndre Stenstue Rende (Plate I) except the fact that clay predominates. The core of the Stortorn horst, however, is composed of the underlying Ældre Yoldia clay, this being the only outcrop of that deposit. The beautifully contorted sands between the two adjacent horsts (3800–4300) simulate the broken overfolds of Martørv Bakker.

The zone of squeezed anticlines represents a zone of greatly increased but localised pressure. The imperfectly preserved structure between the two horsts has the same characteristic as on the iceward side of the Dronningestol up to the Sommerspir, and the dying down of the anticlines away from the centres of greatest compression is similar to that of Møens Klint.



In both areas also the anticlines are separated from one another by thrust-planes, and the roots of the structure are hidden from view.

(v) *Section between Det lille Blaa and Maarup Kirke* (Plate I).

This section may be divided into two parts:

- (a) A disturbed part towards the south-west, between Grotten Point and Maarup Kirke.
- (b) An undisturbed part between Grotten Point and Det lille Blaa to the north-east.

- (a) The termination of the disturbances is seen at Grotten Point. This portion was also the last to be moulded by glacial action. A fine section of the sands associated with streaky clay was seen near Maarup Kirke landslip near 3600, at the big hollow marked on the section. All the intercalated clay suggests differential movement of the various layers of clay and sand.

The last phase of ice-action is shown by the deposition of boulder clay (G).

- (b) The undisturbed part towards the north-east shows the arch of diluvial clay overlain on the leeward side by a little boulder clay and later beds, but on the iceward side by glacio-fluvial sand. The diluvial sand and the upper part of the diluvial clay, as already suggested, have been entirely removed. Hence the top of the clay is a constructional form. Its "greasy," "fatty" surface has formed a major thrust-plane over which the material was transported.

How far the bare surface of diluvial clay extends, denuded of its overmantle of diluvial sands, can only be ascertained by borings.

The cessation of the disturbances at Grotten Point was due to the cessation of the supply of material. That is, that the removal of material from the floor of the ice had a definite limit, and this limit we know from other disturbed areas is determined by the formation of definite gradients, resulting in a plane of movement, over which material transported from much farther afield could readily move.

#### VIII. SUMMARY.

1. The structure of the disturbed deposits of the Lønstrup coast is due entirely to ice-action, and has no connection with earth-movements.
2. The deposits represent the final positions of englacial material after the melting of the interstitial ice.
3. The type of structure is analogous to that seen in decaying Arctic glaciers, and is due to the arresting of movement of the frontal part of an overloaded ice-sheet.
4. The structure has been built up in the reverse direction to the line of movement.
5. The "fish-scale" structure represents the formation of gradients under the influence of tangential pressure.
6. The extent of the disturbances has been influenced by the following factors:—
  - (1) Suitability of material.
  - (2) The supply of material.
  - (3) The size of the ice-sheet.
7. The new topographical feature took the form of a dome-shaped lenticular hill, of drumloid outline.

8. The variation in strike cannot be seen in this area as in others, owing to absence of sections, and the surface mantle of blown sand.
9. The sections fall into three divisions each characterised by particular structures:
  - (1) Towards the south-south-west, a dominance of sand and but few thrust-planes.
  - (2) A central zone of thrust-planes.
  - (3) Towards the north-north-east a zone of squeezed anticlines associated with thrust-planes.
- In (1) the stratigraphical succession is lost.
- In (2) it is generally preserved.
- In (3) it may be seen both in a normal and also in an inverted position.
10. Overthrust of beds occurs repeatedly along thrust-planes, but is especially marked in the central zone.
11. The strike of the beds varies only a little in the whole length of the sections.
12. The inclined beds have a constant direction of dip to the north-north-east or north-east approximately.
13. The direction of dip agrees with that resulting from a movement from the north-north-east towards the south-south-west, and this was the direction of movement of the ice-sheet.
14. The disturbances are local and superficial, and appear to be bounded by the 100-foot contour.
15. The Lønstrup sections have many points of structure similar to that of the disturbed deposits of the Mud Buttes of Alberta.
16. The sections may be regarded as classical examples of a particular type of glacial tectonics; this type I have called "*the stagnant-glacier type*."
17. The isolated masses of clay and sand may be regarded as portions of a once continuous horizontal deposit. This material was incorporated as sheets in the ice and subsequently split up into something like sixty isolated combined units of "sand and clay."

In conclusion I beg to express my grateful thanks to the University of London for a grant from the Dixon Fund for the purpose of carrying out this investigation.

I am also indebted to Dr V. MADSEN, Director of the Danish Geological Survey, for much kindness, and for advising me to visit these classical sections.

To Mrs H. DEWEY I am indebted for the translation of Danish literature, and to State-Geologist AXEL JESSEN for conducting me during a preliminary traverse of the sections, as well as for making arrangements for my stay at Lønstrup.

To Professor W. W. WATTS, F.R.S., I am more than grateful for giving me facilities for the working out of the results, at the Geological Department of the Imperial College of Science and Technology, South Kensington, London.

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## EXPLANATION OF PLATES.

## PLATE I.

Feet. Section between Det lille Blaa and Maarup Kirke.

- 0-2400. Undisturbed diluvial clay forming a mound, the crest of which occurs at 1300. At this point the overlying boulder clay also commences. Diluvial sand is absent.
- 0-1100. Glacio-fluvial sand above diluvial clay.
- 2800-2900. Grotten Point marks the commencement of the disturbances.
3500. Commencement of disturbed diluvial sands with associated lenticles of diluvial clay. Gradual rise of the overlying boulder clay which thins out towards the S.S.W.
- The upper surface of the undisturbed diluvial clay, which dips below the shore-line at Grotten Point, is regarded as a movement plane, over which the disturbed beds have been transported as incorporated englacial material. Grotten Point is regarded as the last phase and final product in the sequence of disturbed phenomena.

Section between Maarup Kirke and Rubjerg Knude Fyr.

- 0-1300. Diluvial sand associated with wedge-shaped masses of diluvial clay.
- The sand-bedding follows concordantly with the clay below, but its upper surface is transgressed by the overlying clay, the line of junction being marked by a thrust-plane.
- 1300-1600. The first squeezed anticline bounded by thrust-planes. The clay differs in structure on the two limbs under the influence of pressure on the inward side and tension on the leeward side. The anticline is in the nature of a compressed "flow-overfold."
- 2200-2300. Moserende. The "core" of the second well-marked anticline. The structure shows inversion of the succession.
2800. The "core" of the third squeezed anticline.
2900. Beautifully rippled sand associated with contortion, in the neighbourhood of a thrust-plane.
- 3200-3400. Anticline, but structure only partially shown.
- 3500-4000. Stortorn. A massive bluff of stiff-bedded clay which acted as a "horst" and led to the initiation of the zone of squeezed anticlines. Ældre Yoldia clay below; slips common.
- 4000-4300. Contorted sands squeezed against clays.
4300. Thrust-plane and position of sigmoid curve.
- 4300-4800. Clay flow-overfolds which formed a "horst" against which the sands were squeezed.

Section between Rubjerg Knude Fyr and Brede Rende.

*"The Zone of Thrust-Planes."*

(Blown sand on the top of the cliffs omitted.)

5100. Double thrust-plane. The clays show contortion.
5800. Contorted sands.
5900. Bedded clays, also seen at 4900 and 6900.
- 7300-7600. Five clay bands with associated sands. These suggest that they represent isolated portions of a once continuous "clay-sand" unit which was subsequently divided along thrust-planes as in Arctic glaciers. The inclination of the thrust-planes is relative to that of the sigmoid curve 7600 of the constructed "horst" 7600-8200.
8200. Very well-marked thrust-plane, between bedded clays and bedded sands. These sands mark a point where the original water bedding of the sands, which has to some extent been preserved up to this point, is now largely destroyed and replaced by a new bedding due to differential thrust movement.
- 8600-9600. Considerable development of sand with drawn-out lenticles of clay, the bedding becoming almost horizontal.

Section between Brede Rende and Stensnæs.

- 9600-10,700. Mostly sand with clay lenticles. The clay has been drawn out and concentrated at 10,600.
- 11,000-11,400. Massive clay with lenticles of sand. At 11,000 the clay forms a sigmoid curve. Hence this mass formed a "horst" against which later beds were compressed.
- 11,400-11,600. A broken syncline.



11,800–12,100. Very fine thrust-plane. The beds forming the sole of the thrust assume a honeycombed structure of clay with galls of sand and in places simulate augen structure.

12,100–12,600. Martørv Bakker.

Initiation of the disturbances. The steep face at 12,600 represents the melted-out bands of englacial material in the stagnant front of an overloaded ice-sheet. The immobility of this part of the ice-sheet initiated the disturbances.

13,500–14,000. Stensnøes. Sands and gravels with shingle resembling morainic material. Worn specimens of *Astarte* and *Macoma* were obtained from the talus-slope.

14,000–14,100. Transported and contorted fine loamy sands with plant remains.

#### PLATE II.

Fig. 1. Section near Martørv Bakker, at the point marked 12,600 in Plate I.

Slightly inclined beds of clay and sand end abruptly, and against the steep face is a deposit of pale grey sandy boulder clay. This point marks the initiation of the types of disturbance described in the paper.

The structure of the inclined beds of clay and sand is analogous to that developed in the lower englacial material, at the stagnant end of a decaying glacier of Arctic type.

Fig. 2. Section near Stensnøes at the point marked 14,000 in Plate I.

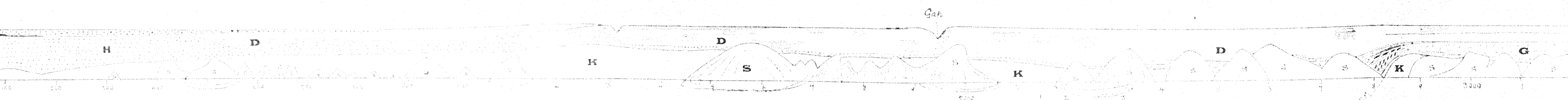
Contorted loamy leaf-bearing sands which pass laterally upwards into water-sorted gravel and sand of morainic type. Worn specimens of *Astarte* sp. and *Macoma* sp. were fairly plentiful in the latter deposit.

Scale vertical and horizontal.

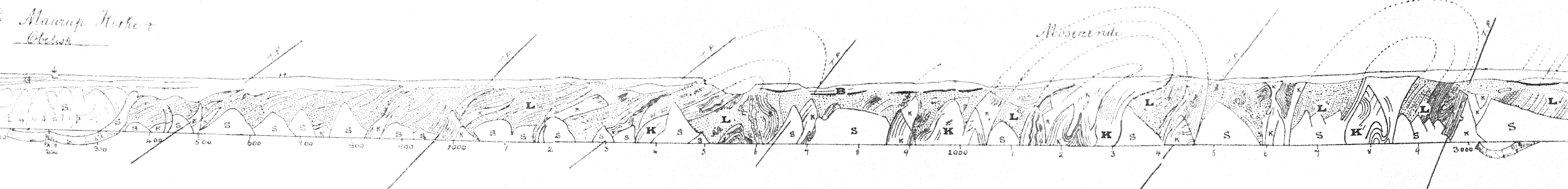


NE. Det lille Blaa.

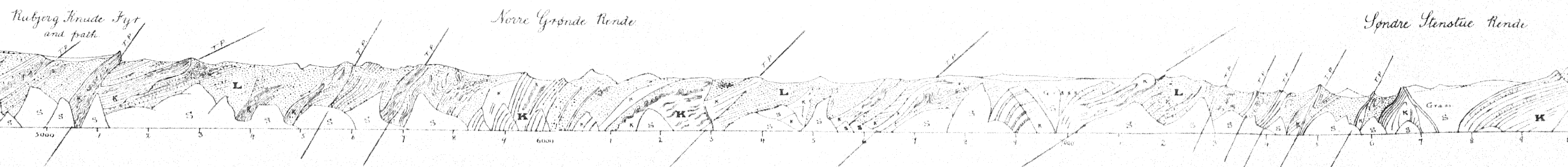
Grotten.



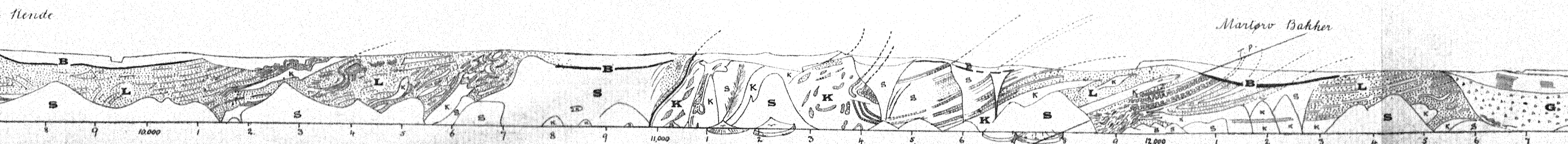
SECTION BETWEEN DET LILLE BLAA AND MAARUP KIRKE.



SECTION BETWEEN MAARUP KIRKE AND RUBJERG KNUDE FYR.



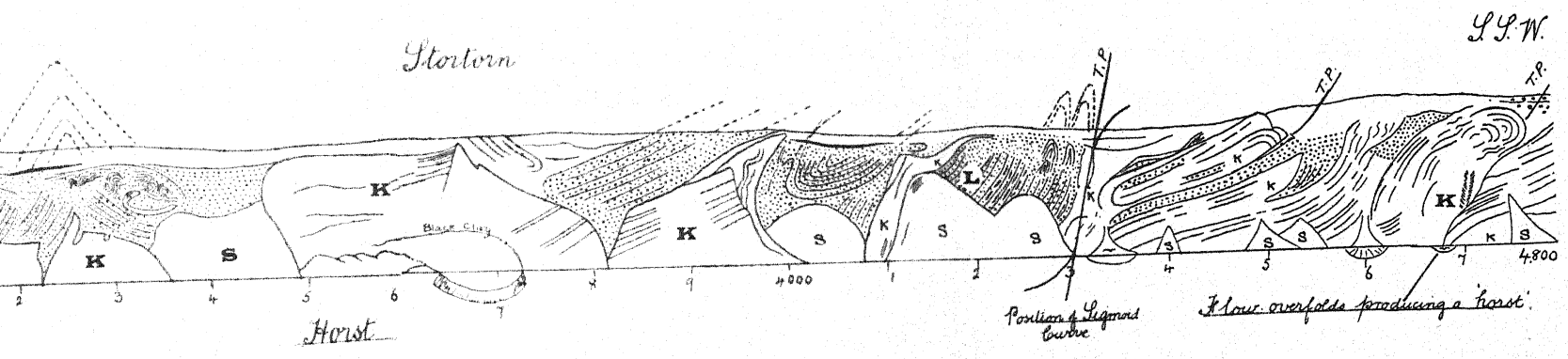
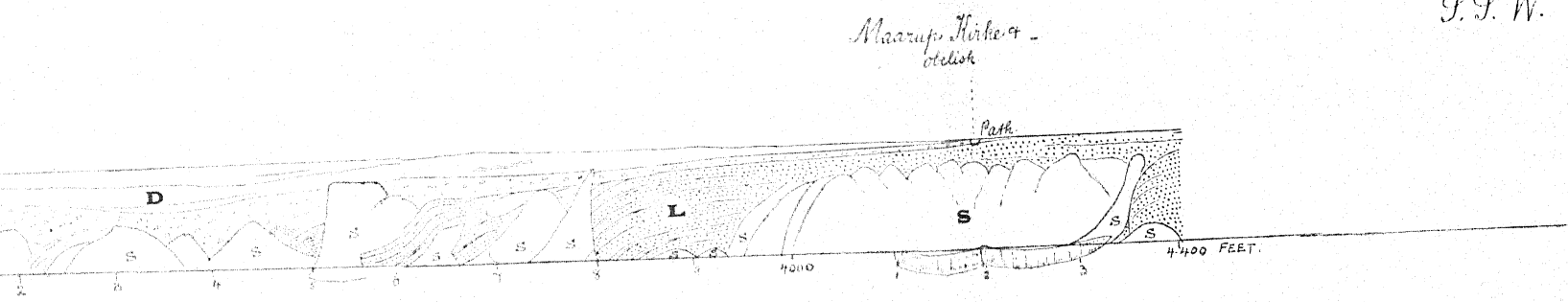
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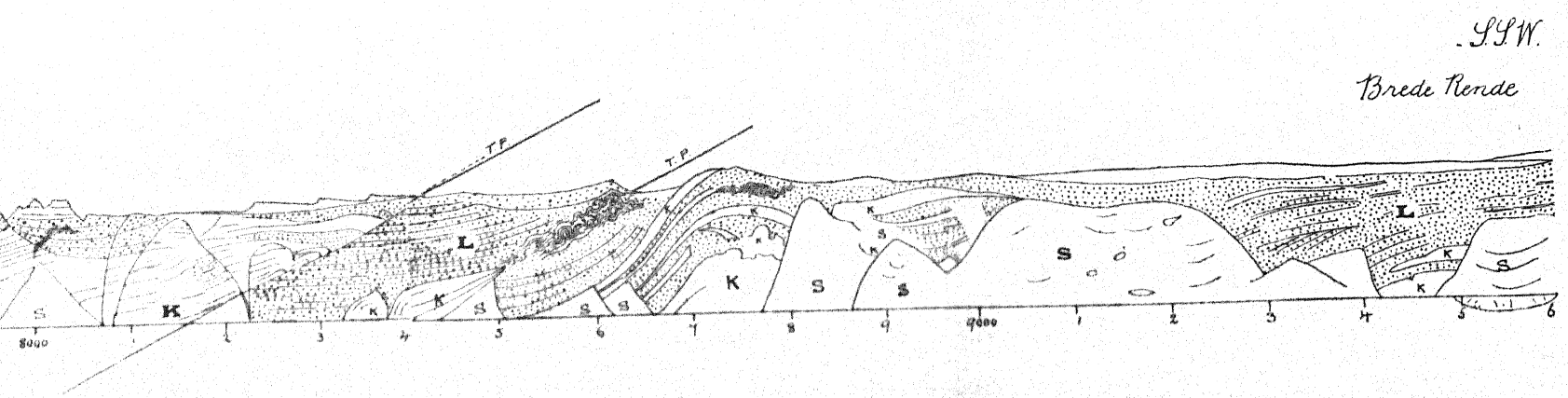
SECTION BETWEEN BREDE RENDE AND STENSNES.

B, Peat. D, Saxicava sand with Yoldia clay above in places. G, Boulder clay (clayey sand with stones). H, Glacio-fluvial gravel or sand. K, Glacial clay without stones. L, Glacial sands, with plant-remains in places. S, Talus. T.P.,

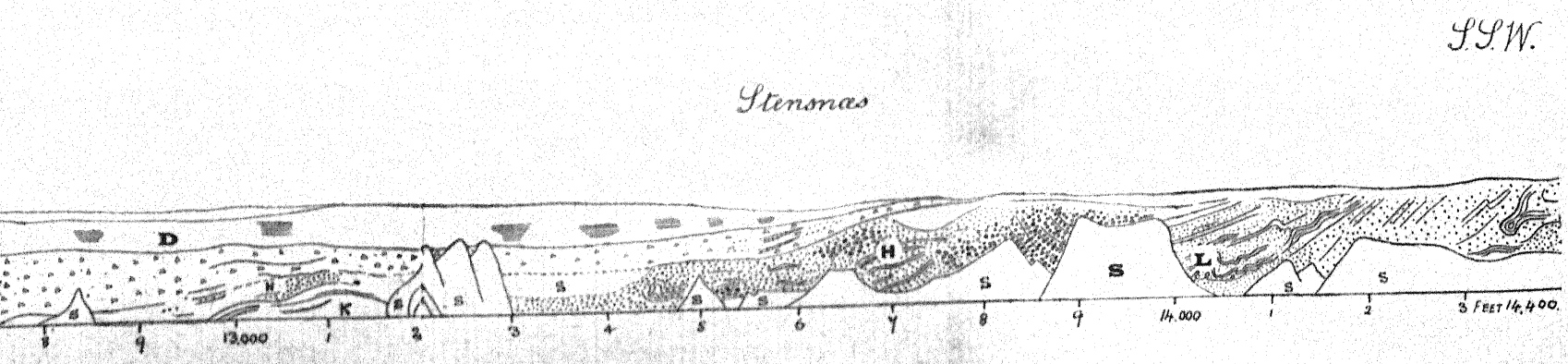
S. S. W.



S. S. W.



S. S. W.



S. S. W.

T.P. = Thrust-plane. Blown sand usually occurs on the top of the cliffs.





Dr GEORGE SLATER on "The Disturbed Glacial Deposits in the Neighbourhood of Lonstrup,  
near Hjørring, North Denmark.—PLATE II.

Near Stensnes,

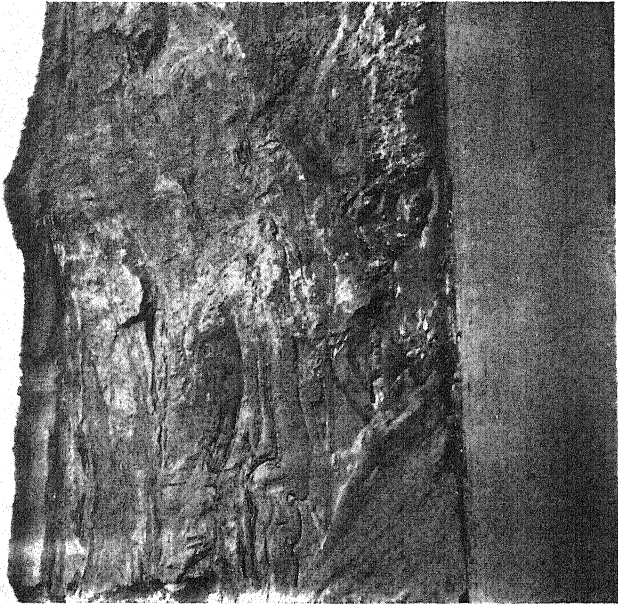


Photo: G. Slater.

FIG. 2.—Contorted loamy sands and clays. Plant-remains found.

Near Martørv Bakker.

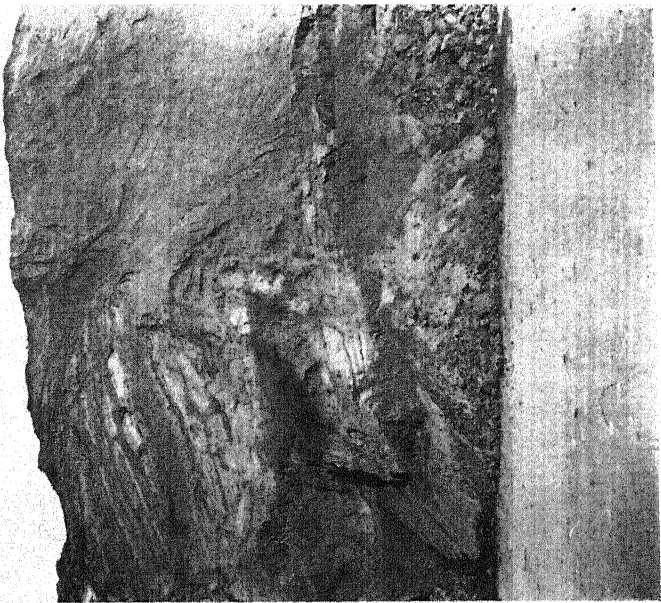


Photo: G. Slater.

FIG. 1.—Steep face of bedded sand and clay with boulder clay lying against the face (see Section 12,600 feet).





## XIV.—The Igneous and Metamorphic History of Cromar, Deeside, Aberdeenshire.

By H. H. Read, D.Sc., A.R.C.Sc., F.G.S. (With Seven Text-figures.)

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## I. INTRODUCTION.

Middle and Lower Deeside lie within the belt of injection and high-temperature metamorphism made famous by the pioneer researches of Mr GEORGE BARROW. In this paper are recorded the results obtained from a study of Cromar, an area small enough to admit of detailed petrographical treatment and yet large enough to exhibit a considerable variety of igneous and metamorphic phenomena. Of the three great phases of igneous activity there displayed, one is older than the epoch of maximum crustal movements, the second is closely connected with these, and the third is later; the rocks of each period have their own quite definite chemical, petrographical, and geological characteristics. Whilst here most attention will be directed towards the second group, that associated with the movements, an account of the other two groups will be given adequate for a discussion of the full igneous history of the area.

The district examined in detail is shown in fig. 1. It is made up of a group of rough hills lying between Tarland and the River Dee. The ground is on the whole well exposed; large bare glaciated surfaces enable the various complexes to be studied with ease.

Of previous researches dealing in particular with the Cromar area there are none. It was briefly described by L. W. HINXMAN [29, p. 11]\* in the *Geological Survey Memoir*, "Central Aberdeenshire," of 1890. Mr HINXMAN drew attention to the injection-phenomena seen at Queen's Hill, and to the west: these he connected with the Coull granite. On the one-inch Geological Survey map, Sheet 66 (Banchory), 1897, the majority of the injection-

\* Figures within square brackets refer to the Bibliography at the end of the paper.

rocks described in this paper are called "granitic gneiss." The Cromar area is placed by G. BARROW [9] within his "sillimanite aureole" in the map illustrating his paper "On the Geology of Lower Deeside, etc.," but it has not been further described by him.

## II. THE SEDIMENTARY SCHISTS.

The succession and structure of the Highland Schists of Middle Deeside are a subject for a separate investigation, but a few remarks applicable to Cromar will be given here. Within

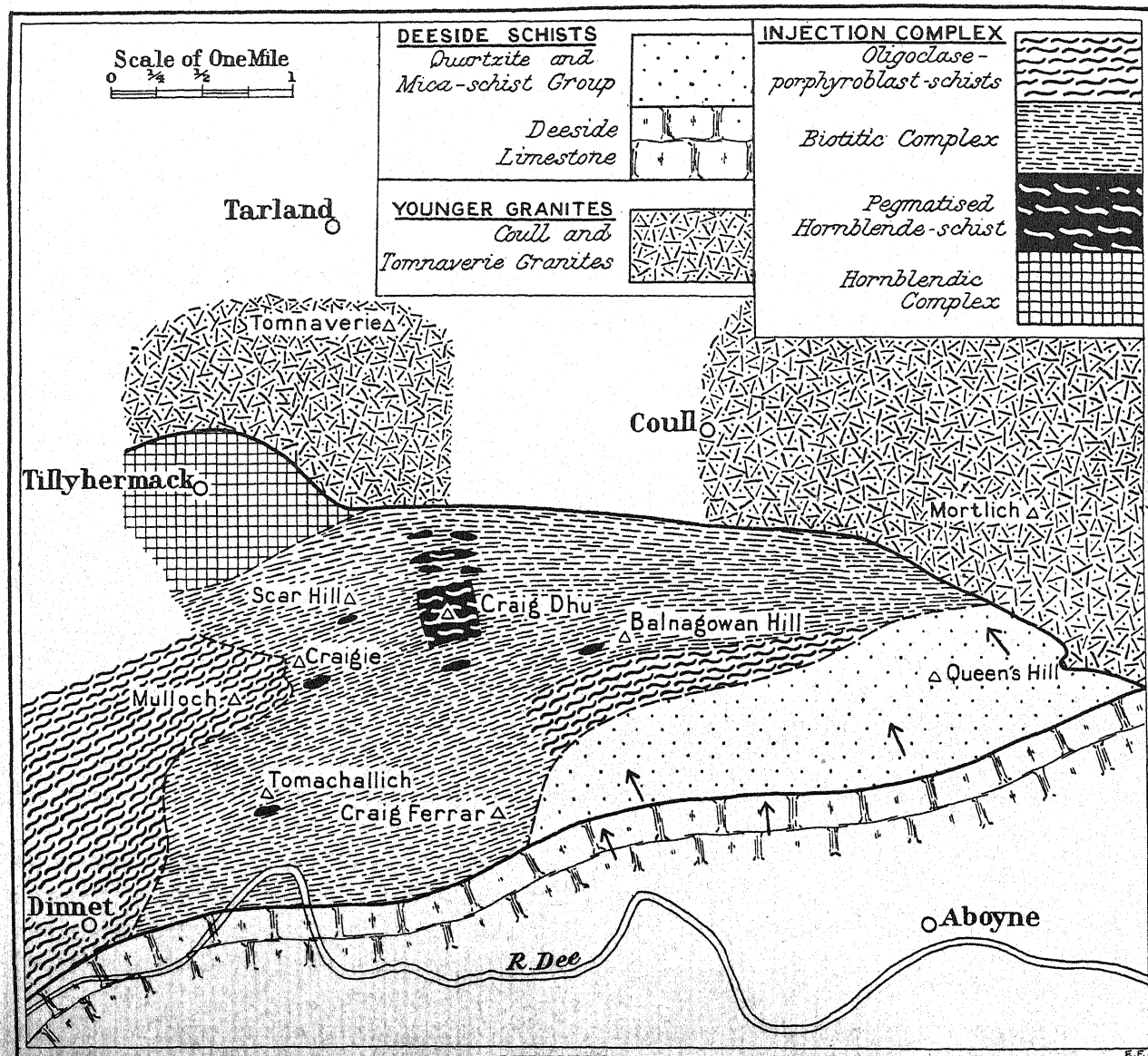


FIG. 1.—Geological Sketch-map of part of Cromar, Deeside.

the limits of the area studied in detail, the metamorphic rocks of sedimentary origin belong to a single group, varying from quartzite to mica-schist. This quartzite and mica-schist group lies structurally above the thick limestone—the Deeside Limestone—which occupies the ground around Aboyne (fig. 1). The injection-phenomena with which this paper is more particularly concerned have their habitat entirely within the quartzite and mica-schist group—the Deeside Limestone thus forms a natural limit to the detailed area.



Over by far the greater part of its outcrop, the quartzite and mica-schist group is mixed in varying degrees with material of magmatic origin, but, fortunately, where it is well exposed in a range of wooded hills running from east of Craig Ferrar to Queen's Hill (fig. 1), it is relatively free from igneous intrusions. Along the strike westwards to Craig Ferrar and at right angles to the strike northwards to Balnagowan Hill, the quartzite and mica-schist group passes, as afterwards described, into a complex of igneous and sedimentary rocks mixed so intimately that they can be mapped only as a unit. In the Queen's Hill belt of comparatively unmixed sedimentary schists there are fairly abundant thin, irregular, often transverse, pegmatites, but nothing resembling injection has been seen here. These pegmatites are like those noted later from the injection-complex (p. 334). Their possible place in the igneous and metamorphic history of the area is discussed on p. 348.

*Petrography.*—The sedimentary schists vary from an almost pure quartz rock to a thoroughly pelitic schist, but the more siliceous types are commonest, and the average composition of the whole group would probably be represented by that of a biotite-quartzite. Thin bands of more micaceous material occur between thick siliceous beds.

The most siliceous type is a *quartzite*, grey or white in colour, and often glassy in appearance. It consists of elongated sutured grains of quartz together with a variable amount of cloudy alkali-felspar grains. Biotite, zircon, and apatite are accessory. In the less siliceous rocks, the *biotite-quartzites*, dark mica becomes a notable constituent in parallel thin plates penetrating the quartz grains; its pleochroism is from pale yellow to dark brown. Colourless mica is not common in stout blades often arranged across the foliation. Zircon, apatite, garnet, and iron-ore are accessory. Micas increase in amount till *quartzose mica-schists* and *mica-schists* arise: in these, biotite occurs as trains of large plates in a base of quartz and scarce alkali-felspar grains; muscovite builds large plates in the coarse quartz-felspathic bands. Of the dozen slices cut from the most pelitic rocks of this group only one contains sillimanite; this mineral occurs as a line of tiny prismatic grains amongst mica felts. The same slice exhibits a considerable amount of pink garnet in large rounded or shapeless grains set in coarse biotite plates.

Almost all the more micaceous rocks of this group display bands or stripes of varying width made up of a fine-grained felt of tiny laths of colourless mica with which is associated much scarcer dark mica. These micaceous stripes run parallel with the schistosity and could be interpreted as original, but certain of their features suggest a different origin. They often present the appearance of springing from a central crack or canal traceable within the micaceous band, and a rough symmetry, in colour-variations, arrangement of the felt, amount of biotite, etc., is observable about this crack. Rocks in which these bands are well developed show two other features of some importance: their biotite is either of a curious brassy colour or else bleached, and their quartz and felspar grains have a marked brownish coating or corrosion of their external surfaces. It appears possible that these micaceous bands, and the bleaching and corrosion just noted, may be due to the passage of potash-bearing and other solutions through the rock, and are thus to be connected in origin with the "shimmer-aggregates" and other phenomena described later on pp. 333-334.

Before this section dealing with the country-rocks is completed, it must be stated that it is a matter for discussion whether a group of rocks—the *oligoclase-porphyroblast-schists*—which this paper is mainly concerned. So far as the evidence goes, the writer considers it better to regard these rocks as intimately connected with the injection-processes, and they are accordingly described with the complex. In order, however, to express the tentative nature



of the writer's conclusions, the account of these rocks is placed in an appendix to the description of the main complex (pp. 338-342).

### III. THE GREENSTONE SERIES.

At many localities in Cromar there occur sheet- or sill-like bodies of hornblendic rocks that represent a series of basic igneous rocks older than the metamorphic period. Such rocks may conveniently be called the *Greenstone Series*; they are, of course, the local representatives of the Basic Older Igneous Rocks of the Geological Survey. In Cromar, hornblendic rocks can be seen especially well on the bare Craig Dhu ridge, and smaller exposures are found on Balnagowan Hill, Tomachallich, Balnacraig (south of Craigie), and on the south face of Scar Hill (see fig. 1, p. 318). It is a difficult matter to find even a small mass of these rocks that is not mixed with intrusive acid igneous material belonging to the injection-period described in the next section, but it is reasonable to believe that the hornblendic parent of these complexes differed originally in no respect from members of this Series lying outside the Cromar area.

Slices have been cut from rocks which show no apparent admixture with later igneous material. In hand-specimens the coarser rocks are dark green and highly crystalline: in slice they are seen to be composed of a granoblastic association of labradorite and hornblende. The felspar is clear: the amphibole has a pale yellow, b deep brown green, c deep green or bluish green. Occasionally a colourless or pale green clinopyroxene is present in small amount. In the fine-grained rocks, the amphibole occurs in prismatic crystals of varying sizes, the smaller being enclosed in the felspar plates.

Since in Cromar the Greenstone Series is almost everywhere intimately mixed with later igneous material, it is necessary to go beyond that area to gather data bearing upon the original character of this series. In the Dalradian region, basic igneous activity anterior to the metamorphism manifests itself either as sill- or sheet-like minor intrusions or as lavas. Pyroclastic rocks belonging to this series may possibly be represented by parts of the Green Beds.

The minor intrusions—the Basic Older Igneous Rocks of the Geological Survey—have been described in detail in most of the Survey Memoirs dealing with the Dalradian region [36]. They form sills or sheets often extending along the strike for great distances; now almost everywhere composed of amphibolites, epidiorites, or hornblende-schists, they exhibit their original character in certain favoured localities, as at Portsoy (Banffshire), where the parent rock of the thicker sills is seen to be normal gabbro, with rarer enstatite-gabbro [41, pp. 91-2]. At Portsoy, as elsewhere in the Dalradian region, serpentines and other ultrabasic types accompany the basic sills; the complementary feldspathic pole of the differentiation from gabbro is shown at Portsoy by a small anorthosite body [41, p. 97].

Whilst, so far as is known, the parent rocks of the Greenstone Series in most of the Dalradian region show little departure from the normal gabbro or doleritic type, yet the lavas and associated intrusions of pre-metamorphism age in the Tayvallich (Argyllshire) district display distinct spilitic characters. Sir JOHN FLETT [20, pp. 50-5; 21, pp. 84-95] has described spilites, with rare soda-felsite, keratophyre, and soda-granite-porphry from Tayvallich. With this suite are found abundant basic rocks whose spilitic affinities are less in evidence. For instance, analyses of the epidiorites of Ardifuar (Argyllshire) [20, p. 55] and of the epidiorite of Portsoy (Banffshire) [41, p. 95] are thoroughly alike, both being of normal gabbroic composition.

With reference to the Cromar area, it may be stated that igneous activity prior to the metamorphic period manifested itself by sill-intrusions of basic igneous rocks which, so far as is known, were of calc-alkalic gabbro composition.

## IV. THE INJECTION COMPLEX.

The second phase of igneous action in Cromar was radically different, both in mode of occurrence and type of rocks, from that just described. It reveals itself in a complex of varied nature resulting from the intimate admixture of acid igneous materials with the sedimentary and igneous rocks of earlier date. That this injection was closely associated with the metamorphic period seems indicated by certain considerations dealt with later (p. 347).

The injection complex may be simply divided into two parts, the one having the siliceous and pelitic sediments as its country-rock, the other having the igneous rocks of the Greenstone Series. The first will be called the *Biotitic Complex*, the second the *Hornblendic Complex*.

A. *The Biotitic Complex.*

Reference has already been made to the difficulties of interpretation of the group of the *oligoclase-porphyroblast-schists*. This group may be regarded as either (1) normal sedimentary schists, or (2) normal sedimentary schists modified by injection-processes and injection-metamorphism. It can be either part of the country-rock or part of the complex. The writer is of the tentative opinion, from the available local evidence and from comparative studies (pp. 339-342), that the oligoclase-porphyroblast-schists are more likely to be part of the injection complex than unmodified sedimentary schists; they are accordingly described as an appendix to the Biotitic Complex.

Concerning the *injection-rocks* proper of the Biotitic Complex there is fortunately no doubt. It is convenient, therefore, to describe these first.

**INJECTION-ROCKS.**—The term *injection-rock* is here applied to the products arising from the injection of igneous material into country-rock. Such rocks can, from the nature of their origin, vary from those possessing dominant country-rock characters to those with dominant igneous characters; they include, likewise, rocks in which the intrusive igneous and country-rock components are readily separable, and rocks in which a more intimate mixture—chemical rather than mechanical—has taken place.

**Field Occurrence.**—A traverse from Craig Ferrar northwards to Craig Dhu and Scar Hill displays very clearly the character of the biotitic injection-rocks. On Craig Ferrar, magnificent exposures show a very variable complex. Lit-par-lit injection of a coarse kind is well developed and, besides, irregular masses of a mafic-poor coarse aplitic rock are common. Everywhere there is much pegmatite and quartz veining. Narrow belts of sediment persist for short distances until they become broken up into xenolithic complexes by the ramification of igneous veins. These sedimentary relics are seen to have been felspathic quartzites and mica-schists like those outside the complex.

Essentially similar phenomena are encountered on the craggy hill, Tomachallich. There is here considerable lit-par-lit injection, but at the summit the complex is dominantly xenolithic. In parts of the hill, soaking by igneous juices has followed certain belts of the invaded rock, leaving thin siliceous films unsoaked. Here again the main xenoliths, as now preserved, are of felspathic quartzite, but there are also many wisps of argillaceous biotite-hornfels. The xenoliths of banded and of schistose sediments lie at all angles in the magmatic matrix. In almost all cases the length of the xenolith coincides with the banding or schistosity. Usually, the longest axes of the xenoliths are oriented in a direction roughly agreeing with the fluxions or lits of the enclosing magmatic rock which are, in turn, in accord with the regional strike as



indicated by the top of the Deeside Limestone. In any exposure of more than a few yards area, however, it is apparent that the longer axes of xenoliths, and therefore their respective bandings or schistositities, are not strictly parallel one with another. As an example there is on Tomachallich a block of about 3 feet cube in which are seen seven xenoliths, the largest 1 foot 6 inches in length; in no two cases were the directions of foliation or banding of the xenoliths parallel, whilst in three adjacent xenoliths they were seen to be all at right angles. Around these diversely oriented xenoliths the magmatic rock appears to flow in sinuous curves.

On the south face of Tomachallich there are many huge aplitic and pegmatitic veins and blotches similar to those of Craig Ferrar.

Resuming our traverse northwards from Craig Ferrar we find somewhat poorly exposed on Chapel Hill (between Craig Ferrar and Craig Dhu) a dominantly xenolithic complex of biotite-rich granitic gneiss with enclaves of siliceous schist, together with less important areas of lit-par-lit injection and some few patches of soaked quartzite.

Most of Craig Dhu consists of pegmatized hornblende-schist as described later on p. 343, but south of a small lochan on the summit ridge there is a narrow belt of siliceous and micaceous sediment lit-par-lit injected and permeated by mafic-poor magmatic rocks; xenolithic complexes are rare. On the northern slopes of the hill is seen much lit-par-lit injection into semi-pelitic biotite-schist and feldspathic quartzite.

On Scar Hill excellent exposures are provided of fluxional biotite-rich igneous gneiss with abundant xenoliths. On the north face the igneous component is more micaceous, with layers very rich in biotite and with wavy films of the same mineral; here the injection is lit-par-lit rather than enclave-contact. Variation in amounts of biotite in adjacent layers gives the magmatic rock a conspicuous banding. There are innumerable cases of xenoliths with good schistosity lying at all angles to one another and to the dominant fluxion of the igneous component.

The western slopes of Craigie are formed of oligoclase-porphyroblast-schist continuing from Mulloch; as these schists are traced eastwards they pass gradually into a xenolithic complex in which the dominant magmatic part is oligoclase-biotite-gneiss. This passage is perfectly exposed on the bare glaciated western slopes of Craigie. Farther to the north-west, near the Pictish Camps, a similar passage from oligoclase-porphyroblast-schists into gneissic xenolithic complex is seen. A fence runs east and west over Scar Hill and forks at its western end; if one follows the north-north-western branch of this fork, which is directed towards Tillyhermack, one can locate splendid exposures about a quarter of a mile from the forking. On the south, the dominant feature is lit-par-lit injection, often taking on an augened, streaky, or even nebulitic, form. Garnets are abundant; siliceous inclusions and beds are spattered with large garnets; pegmatitic patches and veins are conspicuously garnetiferous, whilst the main injection-rock, especially a layered dark-grey biotite-rich variety, is often rich in garnet. Farther north, the lit-par-lit injection-complex gives place to very massive crags of fluxional oligoclase-biotite-gneiss, occasionally with large orthoclase crystals. Streaks and films of biotite, pricked through by large porphyroblastic oligoclases, are of common occurrence. Northwards this biotite complex passes into the hornblende complex described on p. 344.

The description of the field occurrences will be completed by mention of exposures on Balnagowan Hill that show a passage from sediments into oligoclase-biotite-gneiss through injection-rocks of types similar to those just described, and also of the occurrence of streaky oligoclase-biotite-gneisses south and east of Coull House.



*Petrography.*—The Biotitic Complex may be described under half a dozen heads.

1. Sedimentary Schists injected by Igneous Material.
2. Orthoclase-oligoclase-biotite-gneisses.
3. Oligoclase-biotite-gneiss.
4. Xenoliths.
5. Myrmekite and Shimmer-aggregates.
6. Pegmatites.

1. *Sedimentary Schists injected by Igneous Material.*

The most important rocks of this group are those in which the host is pelitic schist; these are described in detail, whilst the nature of the siliceous sedimentary host may be judged from the descriptions of the xenoliths given later.

In the rocks considered here there are dark blue wisps, bands, or streaks of sedimentary

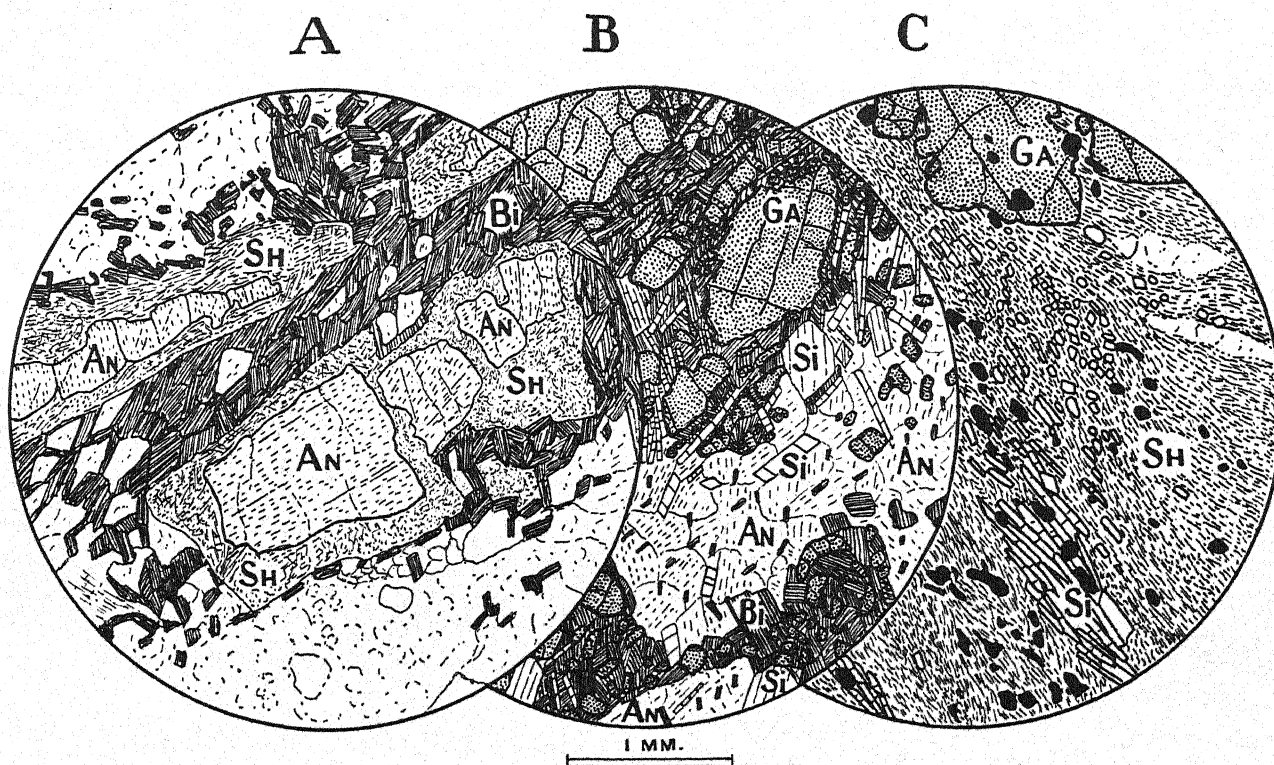


FIG. 2.—Injection-rocks.

- A. *Injection-rock.*—An = andalusite, Sh = shimmer-aggregate, Bi = biotite.  
 B. *Injection-rock.*—Association of garnet (Ga), sillimanite (Si), andalusite (An), and biotite (Bi).  
 C. *Injection-rock.*—Shimmer-aggregate (Sh), around sillimanite (Si), and garnet (Ga). Solid black is iron-oxide.

origin lying between lits or streaks of pale igneous material: in the same hand-specimen it often happens that the rocks become more thoroughly mixed into a biotite-rich rock referred to as oligoclase-biotite-gneiss.

To show the main features of these injection-rocks, a description is given of three thin sections which are figured in fig. 2. All three come from the same locality, the crags already mentioned between Scar Hill and Tillyhermack.

*Specimen A. (fig. 2A).*—Two types of bands are clearly separable. The *igneous bands* consist of quartz and basic oligoclase ( $Ab_{77}An_{23}$ ) either in large clear aplitic grains or in

collections of very small grains. The felspar is sieved with quartz pellets so as to produce a kind of myrmekite. There is a considerable amount of biotite and a few grains of garnet in these bands. A few small patches of muscovite blades occur within the felspars. The *sedimentary bands* are composed of biotite, shimmer-aggregate [G. BARROW, 4, p. 340], andalusite, garnet, and quartzo-felspathic material. The biotite either forms patches of stout blades, with the pleochroism of hornfels-biotite, or else it occurs in finer blades mixed in with quartz and felspar with some colourless mica. Garnet is seen as small, colourless, irregular grains, as if formed by the separation of larger crystals. Andalusite is, however, the most important mineral in these bands; it builds long prismatic crystals, usually arranged parallel to the run of the igneous bands; its pleochroism is a rose,  $h=r$  faint green. Only the central parts of the large crystals are left, and these are always surrounded by a magnificent shimmer-aggregate of colourless mica in tiny blades, which also penetrates along the cracks in the andalusites.

*Specimen B. (fig. 2B).*—The second specimen is a semipelitic schist injected by irregular veins of igneous material carrying large garnets and biotites. In thin section the following bands are seen:—

(a) Large aplitic grains of basic oligoclase,  $Ab_{77}An_{23}$ , with scattered plates of biotite, pleochroic from pale yellow-brown to deep red-brown. There are a few irregular patches of iron-oxide, very scarce quartz, and scattered sillimanite fibres.

(b) At the margin of band *a* there is a layer of very large biotites, followed by a zone of large lensed plagioclases, stout biotite plates, and scattered sillimanite needles. Next come narrow felted streaks of sillimanite needles, biotite, and iron-ores, alternating with biotite-plagioclase streaks with scattered sillimanite needles.

(c) The third band resembles band *a*, except that there are areas thickly scattered with biotite. Both aplitic bands show a very fine-grained shimmer-effect in their felspars.

(d) This band consists of plagioclase, biotite, and sillimanite with spinel grains: sillimanite seems to border small andalusite prisms.

(e) In this band, in other respects like the last, are large eyes (fig. 2B) composed of fragments of garnets between which are sillimanite and andalusite prisms (these two aluminium silicates being often in parallel growth), biotite flakes, green spinel, and doubtful cordierite.

*Specimen C. (fig. 2C).*—This specimen is a dark hornfels injected by garnetiferous aplitic streaks. In slice it resembles that just described in detail. Noteworthy are large garnets which appear as separated fragments. Cracks in the main parts of the garnets are filled with biotite: towards the edges of the garnets are numerous needles of sillimanite, whilst cracks and spaces between the outermost garnet fragments are filled with sillimanite and micas which pass into a large mass of sillimanite and shimmer-aggregate. A garnet in an aplitic band appears to have been separated into parts between which occur biotite and felspar. Some narrow bands in this rock are formed of sillimanite, shimmer-aggregate, black ore (? spinel), and biotite flakes, whilst others have largish oligoclases in addition. Much of the biotite in the sedimentary bands and much-mixed bands is chloritised, whilst in the aplitic bands the oligoclases often show a minute patchy shimmer-effect by the occurrence of tiny pale micas.

Such injection-rocks as these are important in the discussion of the origin of the Biotitic Complex (see p. 335).

## 2. Orthoclase-oligoclase-biotite-gneisses.

Rocks which, in hand-specimen, show a good small-scale augen structure and in slice are seen to be rich in potash-felspar, occur at the margin of the Biotitic Complex against the Hornblendic Complex of Tillyhermack. Allied types are found on Craig Ferrar.



In thin section, these rocks show orthoclase, oligoclase, myrmekite, quartz, and biotite. The potash-felspar forms large shapeless elongated grains and subhedra; it encloses euhedral oligoclase crystals and quartz grains; perthitic streaking is common, and a patchy microcline twinning is occasionally seen. Oligoclase builds large lenses or subhedra. Quartz occurs in two ways, either in areas of large grains associated with large oligoclases or else in areas of tiny grains associated with tiny feldspars and biotites. Myrmekite is abundant in large masses, often springing from the fine quartzo-felspathic layers and invading orthoclase (fig. 3B). Some micaceous quartzo-felspathic layers pass into myrmekite-like layers with a biotite backing (see p. 333). Biotite is present either as large plates with coarse quartz and feldspar, or

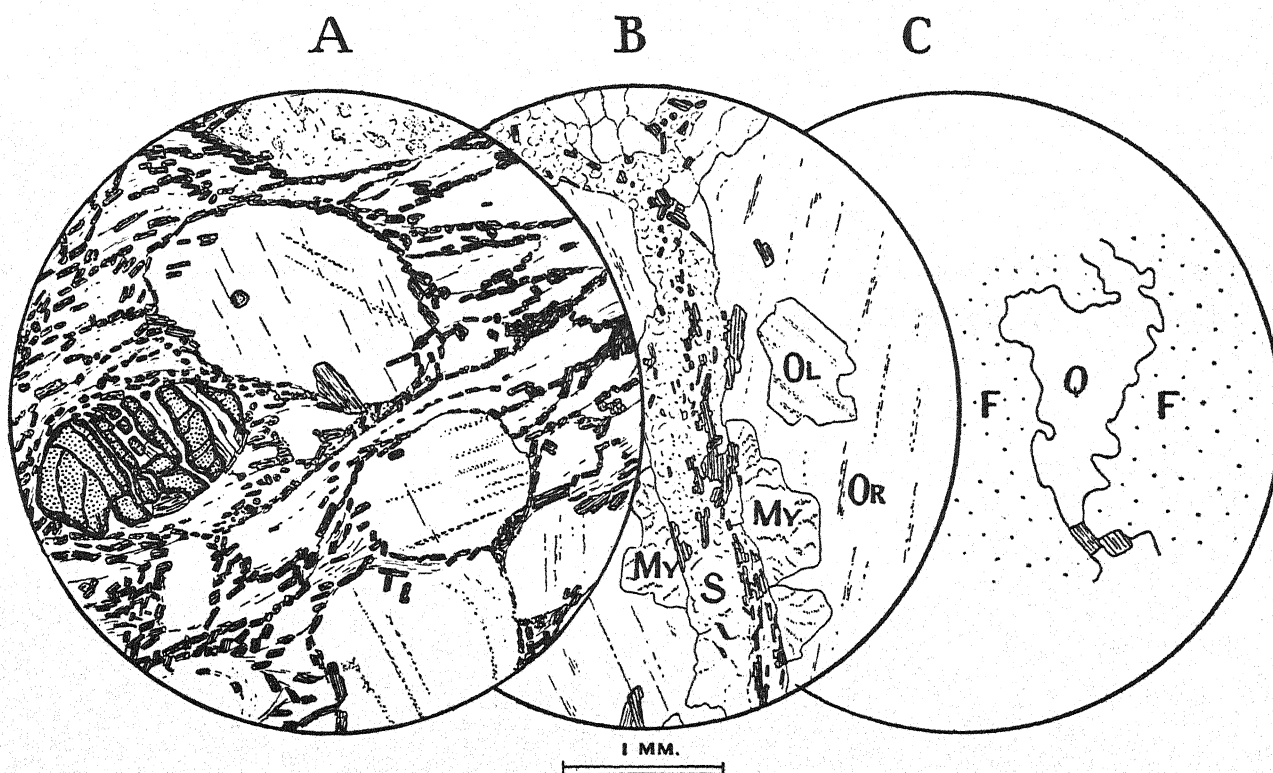


FIG. 3.

- A. *Oligoclase-porphyroblast-schist*.—Eyes of oligoclase in a base of quartz and biotite; fractured garnet on left.  
 B. *Orthoclase-oligoclase-biotite-gneiss*.—OR = orthoclase, OL = oligoclase, MY = myrmekite, S = relic sedimentary band.  
 C. *Suturing of quartz (Q) and feldspar (F) in orthoclase-oligoclase-biotite-gneiss*.

else as tiny plates in the fine-grained quartzo-felspathic streaks. The rock is thus formed of lenses of very coarse-grained feldspar, quartz, and biotite, wrapped about by discontinuous felts of very tiny feldspar, quartz, and biotite which presumably represent altered sedimentary material. Especially characteristic of these rocks is the wavy suturing (fig. 3C) of quartz and feldspar similar to that seen in certain granites and gneisses of Fennoscandia [31, p. 77].

The microaugen orthoclase-oligoclase-biotite-gneiss described above has been analysed; the result is given, with other analyses, in Table A, p. 326.

An inspection of the analyses given in Table A shows the close chemical similarity between the Cromar rock and certain augen gneisses from Stavanger described by V. M. GOLDSCHMIDT [24, pp. 91–9]. The Norwegian rocks are also microscopically very like the Scottish augen gneiss, as can be seen by a comparison of fig. 3B of this paper with the figures given by GOLDSCHMIDT [*e.g.* 24, Pls. XI, XII, and XIII]. The Bru gneiss is considered by GOLDSCHMIDT [24, p. 115] to have been formed from the average phyllite by the addition of 34 per cent.



silica, 2 per cent. lime, 3.3 per cent. soda, and 2.3 per cent. potash, and the subtraction of 2.6 per cent. water, but he admits that a direct impregnation with felspar may have taken place also. The origin of the Rosholmen gneiss is taken to be very uncertain. It can be said

TABLE A.  
*Augen Gneisses.*

	I.	A.	B.
SiO <sub>2</sub>	66.40	66.52	68.27
Al <sub>2</sub> O <sub>3</sub>	14.69	14.86	14.30
Fe <sub>2</sub> O <sub>3</sub>	1.00	1.92	1.02
FeO	3.40	3.96	3.80
MgO	1.04	0.67	0.55
CaO	2.98	1.82	2.18
Na <sub>2</sub> O	3.06	3.29	3.45
K <sub>2</sub> O	4.25	5.42	4.72
H <sub>2</sub> O+	0.90	0.95	0.96
H <sub>2</sub> O—	0.90	0.20	0.04
CO <sub>2</sub>	nil.	trace	0.33
TiO <sub>2</sub>	1.00	0.55	0.45
P <sub>2</sub> O <sub>5</sub>	0.20	0.12	0.14
S	nil.	0.02	0.03
MnO	0.05	0.09	0.07
BaO	..	..	0.13
ZnO	0.15	..	..
Totals	100.02	100.39	100.47

- I. *Microaugen orthoclase-oligoclase-biotite-gneiss*, Dinnet, Aberdeenshire. *Anal.*, W. H. HERDSMAN.  
 A. *Gneiss (mica-rich augen gneiss)*, Bru, Norway. *Anal.*, O. RÖER [in V. M. GOLDSCHMIDT, 24, p. 93].  
 B. *Gneiss (augen gneiss)*, Rosholmen, Norway. *Anal.*, O. RÖER [in V. M. GOLDSCHMIDT, 24, p. 96].

for the Cromar rocks, at all events, that there are tenuous sedimentary wisps lying between felspathic material, and that the rock probably results from the injection of granitic material into pelitic rocks. These orthoclase-rich gneisses are quite subordinate in the Cromar Complex.

### 3. *Oligoclase-biotite-gneiss and Associated Types.*

The rocks now to be described are by far the dominant type in the Biotitic Complex. The oligoclase-biotite-gneiss is a biotite-rich granitic rock showing a more or less well-expressed fluxional or microaugen structure, combined with a coarser layering or streaking due to variations in biotite-content. These structures are parallel with the lit-directions and, on the whole, with the regional strike. These rocks show few or no cataclastic structures. In colour, the oligoclase-biotite-gneiss is always a shade of grey, light when biotite-poor, dark when biotite-rich.

In the most widespread type of oligoclase-biotite-gneiss (fig. 4A), the component minerals are quartz, oligoclase, and biotite, with less abundant sillimanite, garnet, shimmer-aggregate, and muscovite. Common in certain varieties are potash-felspar, myrmekite, and andesine. Accessory are iron-ore, apatite, zircon, and epidote. The structure is gneissic.

Quartz occurs in lenticular patches resolved under crossed nicols into collections of small grains: there is a fairly well-marked strain-polarisation, but not the wavy extinction characteristic of cataclasis. Oligoclase, about Ab<sub>30</sub>An<sub>20</sub> or slightly more calcic, forms large auge-shaped or subhedral areas with undistorted fine twinning. Orthoclase is rare in this

type: occasionally it builds smallish (? corroded) grains. Grains of *myrmekite* are often seen especially in or near certain fine-grained quartzo-felspathic layers (see p. 332). *Biotite*, in almost uniaxial stout plates, wraps round the feldspars or builds streaks of aggregated laths: the pleochroism is pale-yellow to deep reddish-brown.

Noteworthy components of the oligoclase-biotite-gneiss are sillimanite and garnet. *Sillimanite* occurs as colourless blades or prisms of normal optical characters: it is seen in three forms: (1) rare prisms enclosed in feldspar and showing no shimmer-aggregate, (2) a few collections of needles, and (3) by far the most abundantly in fragmental prisms or grains surrounded

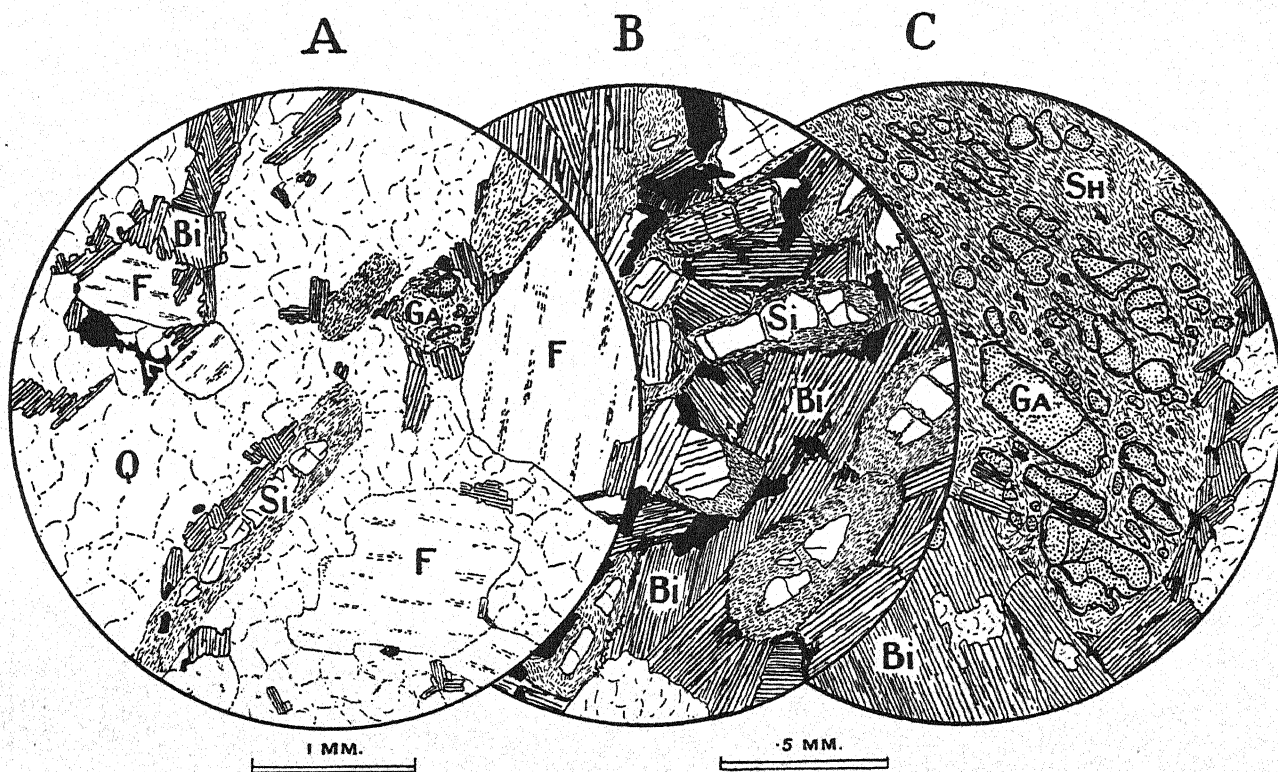


FIG. 4.—Oligoclase-biotite-gneiss.

- A. Quartz (Q), oligoclase (F), and biotite (Bi) are the main constituents. Sillimanite (Si) and garnet (GA) surrounded by shimmer-aggregates. Solid black is iron-oxide.  
 B. Sillimanite (Si) surrounded by shimmer-aggregates, and associated with biotite (Bi) and iron-oxide (solid black).  
 C. Garnet (GA) surrounded by shimmer-aggregate (Sh). Bi=biotite.

by a broad shimmer-aggregate (fig. 4B). *Garnet* appears to occur in two forms, either as large pinkish crystals showing no shimmer-aggregate or as large crystals, broken, cracked, and separated, set in a mass of shimmer-aggregate and tailed with biotite (fig. 4C). Some large patches of shimmer-aggregate show only tiny relics of garnet. Biotite flakes occur in cracks in the garnet and amongst the shimmer-aggregate. The shimmer-aggregate consists of extremely fine colourless mica needles, and has in most cases a lenticular shape with a kernel of sillimanite or garnet. Occasionally, the shimmer-aggregate is seen to pass into stouter plates of colourless mica. In addition to these examples of shimmering, there are often patches and bands of extremely fine-grained shimmer-substance in the feldspar, which in such cases shows corroded borders.

In almost every slice of the oligoclase-biotite-gneiss there are noted streaks of fine-grained quartz-feldspar mosaic which occasionally appears to have been reconstituted into a *myrmekite*-like intergrowth (see p. 332). In these areas, which are undoubtedly relics of the



country-rock, muscovite is often seen, and this mineral, associated with quartz, is common in certain streaks.

Before passing on to consider variants of the oligoclase-biotite-gneiss, we may note that when the igneous and sedimentary mixtures, described on p. 323, pass into more homogeneous magmatic types the resulting rocks are very rich in biotite. For instance, a slice cut from the other end of the small specimen of injection-rock, described on p. 323 as Specimen A, shows a homogeneous magmatic rock consisting of large rounded or lenticular oligoclases, quartz areas, pale-yellow to red-brown biotite in large plates collected together into patches or streaks, small garnets, and large apatites. There are big areas of quartz-felspar mosaic, often submyrmekitic in form, suggesting partly reconstructed sedimentary wisps.

Another slice seems to be of a rock midway between oligoclase-porphyroblast-schist and oligoclase-biotite-gneiss. It is a layered dark grey streaky rock made up of very large lenticular oligoclases, areas of quartz grains, and streaks and patches of biotite. Iron-ore, apatite, zircon, and orthite are accessory.

Certain of the biotite-gneisses of this group contain a plagioclase felspar more calcic than the dominant oligoclase. For instance, a rock from north of Craig Dhu is a coarse augened rock composed of large subhedral or euhedral crystals of andesine (approximately  $Ab_{60}An_{40}$ ), biotite, and very scarce quartz. This rock, which in some respects recalls the sedimentary calc-silicate mica-schists [25, p. 21; 43, p. 138] is undoubtedly magmatic. Again, a slice of the magmatic part of a xenolithic complex of pelitic schist and igneous rock from Scar Hill is seen to be composed of acid labradorite (about  $Ab_{50}An_{50}$ ) in large fresh irregular grains fitted together with quartz. In all cases the felspar is filled with inclusions of quartz in blebs and long tubules: sometimes the quartz is in regular graphic forms. The drop-structure of the quartz-felspar is so fine that often it is difficult to determine the enclosed mineral: while quartz is the dominant drop, it is possible that a more alkalic felspar is sometimes included as drops within the labradorite. Biotite is abundant either as large plates, or as a series of stoutish blades, which, together with parallel layers of quartz, appear to indicate the original schist structures. Pink garnet is common enclosing biotite plates; some crystals are solid euhedra, whilst others are broken up and the spaces filled with the quartz and biotite of the main part of the rock. Black iron-oxide, apatite, and zircon are accessory.

The origin and significance of the quartz pellets in the labradorite are subjects of considerable interest. They are best interpreted, it appears, as being thrown out of combination during the change of a pre-existing more sodic plagioclase (the dominant plagioclase of the biotite-gneisses is oligoclase) into labradorite; they are thus a form of myrmekite, but result not from the replacement of potash by soda and lime as in normal myrmekite (see p. 332), but by the relative increase of lime in the felspar substance. It will be shown later (p. 346) that in some cases the hornblende-schists within the complex are conspicuously biotite-bearing, and it may be suggested that the presence of biotite indicates a transfer of potash into the hornblende-schist. The passage of any hornblende into biotite sets free lime which is then able to combine with the original felspar to increase the anorthite content, but there is no evidence available from the labradorite-biotite-gneiss that this has happened. Further, the occurrence of quartz-blebbing in certain anorthite-hornblende-rocks apparently free from biotite (p. 331) suggests that potash transfer is not operative in such cases. In the gneiss under discussion it is difficult to decide, without detailed micrometric and optical study, whether there has been an actual loss of soda or an actual addition of lime in the felspar. It is thus impossible at present to state which transfer occurs or whether both take place. The subject is worthy of further investigation.



Analyses of two typical oligoclase-biotite-gneisses are given in Table B. The rocks analysed are composed of quartz, oligoclase, and biotite, with fairly common garnet and sillimanite surrounded by shimmer-aggregates.

TABLE B.  
*Oligoclase-biotite-gneisses, etc.*

	I.	II.	A.	B.	C.	D.	
SiO <sub>2</sub>	63.24	66.30	67.3	62.41	65.93	71.36	SiO <sub>2</sub>
Al <sub>2</sub> O <sub>3</sub>	17.27	16.36	15.3	15.01	16.52	13.31	Al <sub>2</sub> O <sub>3</sub>
Fe <sub>2</sub> O <sub>3</sub>	1.50	0.77	..	1.56	4.00	0.99	Fe <sub>2</sub> O <sub>3</sub>
FeO	6.56	6.12	7.8	5.39	2.61	3.36	FeO
MgO	2.00	1.84	1.5	2.74	2.02	0.87	MgO
CaO	2.02	1.90	2.0	2.88	1.76	2.85	CaO
Na <sub>2</sub> O	2.43	2.29	3.9	2.12	2.50	3.58	Na <sub>2</sub> O
K <sub>2</sub> O	2.15	2.58	2.3	3.09	3.31	2.26	K <sub>2</sub> O
H <sub>2</sub> O+	1.80	0.92	..	2.45	} 1.68 {	0.45	H <sub>2</sub> O+
H <sub>2</sub> O—	0.55	0.45	..	0.22		0.25	H <sub>2</sub> O—
CO <sub>2</sub>	nil.	nil.	..	0.77	..	..	CO <sub>2</sub>
TiO <sub>2</sub>	0.33	0.30	..	0.95	..	0.34	TiO <sub>2</sub>
P <sub>2</sub> O <sub>5</sub>	0.03	0.07	..	0.22	..	0.21	P <sub>2</sub> O <sub>5</sub>
S	0.05	trace	..	0.02	..	..	S
MnO	0.15	0.08	..	0.06	..	0.10	MnO
Totals	100.08	99.98	(100.1)	99.89	100.33	99.93	Totals
" C "	7.3	6.3	(2.75)	5.00	(5.71)	0.0	" C "

I. *Oligoclase-biotite-gneiss*, Craigie, Dinnet, Aberdeenshire. *Anal.*, W. H. HERDSMAN.

II. *Oligoclase-biotite-gneiss*, Craigie, Dinnet, Aberdeenshire. *Anal.*, W. H. HERDSMAN.

A. *Granite with much Biotite*, La Grande Carrière, Dièlette, Flamanville, France. *Anal.*, A. LECLÈRE [34, p. 4; *Anal. B.*, p. 7].

B. "*Basic Gneiss-granite*," Flateby-Wald, Nesodden, Oslo. *Anal.*, O. A. BROCH [11, p. 99].

C. "*Mixed Rock*," Metzdorf, Erzgebirge. *Anal.*, R. REINISCH [22, p. 354].

D. *Oligoclase-granite*, Orijärvi, Finland. *Anal.*, P. ESKOLA [17, p. 41].

The analyses of the two oligoclase-biotite-gneisses from Dinnet are essentially alike. Their main features are the high alumina and high ferrous oxide, as is shown by comparison with the typical oligoclase-granite of Orijärvi, Finland (Analysis D). On the other hand, they are not markedly different from certain granitic rocks from continental complexes; for example, they resemble the analysis (A) of a granite from the Flamanville complex stated by LECLÈRE to contain much biotite; again, they are closely comparable with an oligoclase-biotite-gneiss (Analysis B) from the Nesodden, Oslo, complex, and with an Erzgebirge mixed rock (Analysis C) resulting from the injection of granitic material into pelitic sediment. These comparisons are considered later (p. 334), when the origin of the Cromar rocks is discussed.

The exceptional chemical composition of these Dinnet oligoclase-biotite-gneisses, considered as igneous rocks, can be best brought out by use of the corundum value in the norms, which expresses the excess alumina after satisfying the alkalis and lime for the production of feldspars. The symbol for the rock of Analysis I is II.3(4).2.3, and of Analysis II is "II.3".2.3. The norm of Analysis I shows 7.3 per cent. corundum, of Analysis II, 6.3 per cent. corundum. In WASHINGTON'S Tables [51] there are 539 analyses of rocks belonging to the

sodipotassic subrangs of the domalkalic rangs of the order and class into which the Dinnet rocks fall and of those adjacent to this order and class. In all cases except two, normative corundum is absent, negligible, or small; the exceptions are, first, a porphyry from La Creuse, France, with corundum=7.45, concerning which WASHINGTON [51, p. 191] notes " $\text{Al}_2\text{O}_3$  high?" and, second, a Lausitz, Saxony, granite with corundum=6.63. The normative corundum values of the rocks of Table B are shown as "C" beneath the analyses.

The high normative corundum value of the Dinnet rocks corresponds with the presence in the actual rock of much biotite, a notable amount of sillimanite and of garnet, and of the colourless sericitic mica of the shimmer-aggregates. After all the lime has been combined to give the anorthite molecule and garnet, the alumina, iron-oxide, and magnesia are allocated to potash to give biotite, thus reducing any potential potash-felspar; the excess of potash over that required by the biotite is combined with the excess alumina to give muscovitic micas—so that no potash-felspar appears in the mode of these rocks (*cf.* P. ESKOLA [17, p. 60]).

#### 4. *Xenoliths in the Biotitic Complex.*

The dominant xenoliths now seen in the Biotitic Complex are siliceous in character; pelitic xenoliths are represented in most cases by mere wisps of blue hornfels; one xenolith proves to be of an impure limestone. Many xenoliths are hornblendic and are basic igneous rocks caught up in the complex. These xenoliths are now described in order.

The *siliceous xenoliths* are of greasy-looking banded felspathic quartzites showing in thin slices sutured grains of quartz, streaks of small basic plagioclase grains, and colourless to red-brown biotite as their main components. Garnet is common in small round grains: sphene, apatite, zircon, and magnetite are present in accessory amount. Hornblende, pleochroic in pale shades of green and bluish-green, forms prismatic plates sieved by quartz and felspar: the amphibole is often intimately associated with felspar in certain bands. In one slice scapolite occurs towards the edges or along the twin-lamellæ of the felspar (fig. 5B). In addition to showing almost complete scapolitisation, the felspars are often filled with epidote grains; in some cases it appears as if the original felspathic bands are replaced by a mixture of hornblende, garnet, zoisite, epidote, and scapolite.

*Xenoliths of argillaceous rocks* are difficult to extract from the complex, so that few slices are available. In one from Tomachalich, there are fragmental garnet and sillimanite (the latter in long prismatic shreds) lying in great masses of shimmer-aggregate in which occur streaks of biotite. In some cases the garnets are chloritised, whilst the biotite is often totally destroyed to give chlorite and sagenite. Sericitised felspars are not common; there may be scarce new albite mixed with these.

A slice from Craig Ferrar contains staurolite. The rock is very coarse: the main part consists of large plates, with bands of smaller plates, of colourless mica and colourless to red-brown biotite. The two micas are often intergrown. Staurolite occurs in large prisms (fig. 5A) abundant in certain layers: it appears to be streaked out into sillimanite films and layers of very fine needles associated with pale mica. Magnetite and apatite are accessory.

A rare xenolith is a pale-grey coarse *calc-silicate-rock*. In slice it is seen to consist of very large poikiloblastic plates of diopside and hornblende with considerable labradorite and quartz. Sphene, zircon, and vesuvianite are common. The hornblende has a colourless, h=c faint green, and is intimately associated with the colourless diopside. The plagioclase shows a certain amount of shimmering. The structure is poikiloblastic granular. The rock is derived from an impure limestone.



A striking type of *hornblende xenolith* is a pale-grey rock in slice seen to be a granoblastic sieved mixture of hornblende and anorthite. The amphibole forms prismatic grains or poikiloblastic plates with a pale yellow, b green with a brown tinge, c green with a blue tinge; it is sieved with felspar and quartz pellets. The felspar builds limpid water-clear grains, each one filled with pellets of quartz, sometimes in submyrmekitic fashion. Quartz occurs as pellets or tubules in felspar (fig. 5C), or as pellets in hornblende. In one type of these hornblende-anorthite-rocks, biotite in scarce laths, with hornfels-biotite pleochroism, has been noted. In this rock, also, two forms of amphibole are found. The first type has a pale yellow, b=c brown-green, and is untwinned; the second type is almost colourless and shows excellent

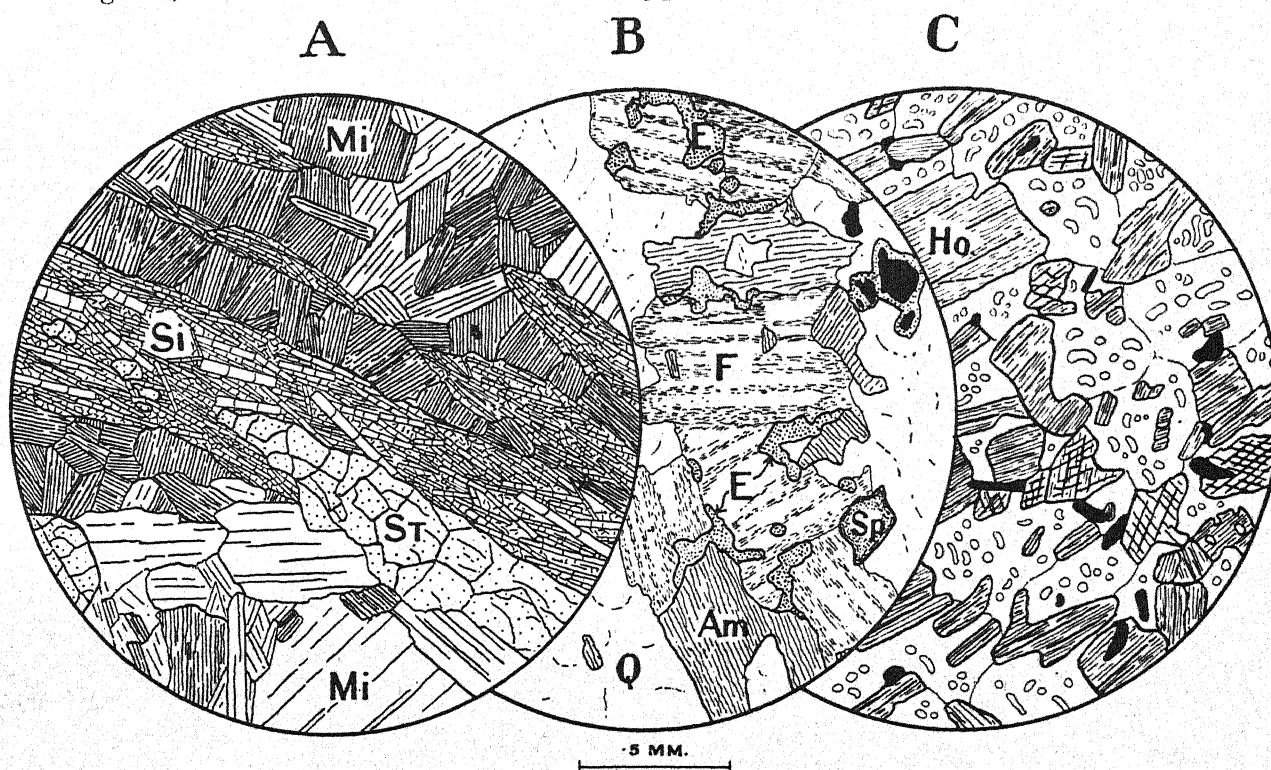


FIG. 5.—Xenoliths in Oligoclase-biotite-gneiss.

A. *Pelitic Xenolith*. Mi=mica, St=staurolite, Si=sillimanite (with some shimmer-aggregate).

B. *Siliceous Xenolith*. Q=quartz, E=epidote, Sp=sphene, F=partly scapolitised felspar, solid black=iron-oxide.

C. *Hornblende Xenolith*. Ho=hornblende, between which are colourless grains of anorthite blebbed by quartz pellets. Solid black is iron-oxide.

lamellar twinning. The two forms are intimately associated, a single crystal often showing both in different parts. The colourless hornblende is exactly like one described from the contaminated rock of Kinharrachie Type from Arnage, Aberdeenshire [42, p. 466]. In another specimen of these hornblende-anorthite-rocks, garnet occurs in large pink euhedra, sometimes so much sieved by the other components that mere skeletons of garnet substance are left: the scarce plagioclase is bytownite-anorthite. Some types of this group of xenoliths show large hornblende and basic plagioclase porphyroblasts lying in a very fine-grained ground mass of tiny hornblendes, scarce biotite, quartz grains, and magnetite.

The quartz-blebbed felspars of the first type of hornblende xenoliths described in the preceding paragraph recall the similar features already mentioned in the labradorite-biotite-gneiss (p. 328). The hornblende xenoliths showing quartz-blebbing in perfection are composed of hornblende, anorthite, and quartz blebs; biotite is absent or extremely rare. The separation of the quartz blebs follows on a relative increase of lime in the felspar. Whether



or not this means an actual loss of soda from the felspar substance has not been determined, but if this has occurred it is possible that the soda has been taken up in the hornblende. Similarly, if actual lime is required to produce anorthite from the originally more sodic plagioclase, it can be derived from the amphibole. The hornblende of these blebbed rocks should then be relatively richer in soda and poorer in lime than the original hornblende. If, however, the possibility of importation of material in solutions into the xenolith be admitted, then such solutions might contain soda and lime, as in the myrmekitic replacement of potash-felspar (see p. 332), but here the lime has been taken up by the original plagioclase whilst the soda has been fixed by the amphibole.

Quartz-blebbed plagioclases apparently exactly similar to those of these xenoliths have been described by B. ASKLUND [1, p. 408] from the biotite-bearing marginal facies of a Swedish amphibolite, and by O. A. BROCH [11, pp. 144-8] in a plagioclase-biotite-gneiss from Nesodden, Oslo. BROCH considers the process to be primarily dependent upon the formation of biotite from hornblende by an importation of potash, with the consequent setting free of anorthite constituents from the amphibole. In the Cromar case just described and discussed there is no biotite and a potash transfer seems inhibited. There are, however, many xenoliths composed of anorthite (without conspicuous quartz-blebbing), hornblende, and a small amount of biotite—in these rocks possibly the operations resulting from a potash transfer, as suggested by BROCH, may have operated. The possible variations in the composition of amphiboles may be wide enough, however, to permit of the formation of anorthite and biotite without invoking a potash transfer.

##### 5. *Myrmekite and Shimmer-aggregates.*

In the description of the Biotitic Complex many references have been made to myrmekite and to shimmer-aggregates. It is proposed now to consider these two subjects in a more connected fashion.

1. *Myrmekite*.—True and undoubted myrmekite is extremely abundant in the Biotitic Complex (see pp. 325, 327), but there is a form of intergrowth of quartz and felspar which often mimics myrmekite. This intergrowth is seen in the fine-grained quartzo-felspathic layers that represent reconstructed sedimentary bands. In these, quartz and felspar have been recrystallised so that the originally separate grains now either touch one another or have the same optical orientation, whilst, in the case of the quartz, there is a tendency for tubular shapes to arise. True myrmekite, however, is readily distinguished from such associations; it invades orthoclase in cauliflower-shaped protuberances, and is based either upon oligoclase or on the fine-grained quartzo-felspathic stripes just considered (fig. 3B, p. 325).

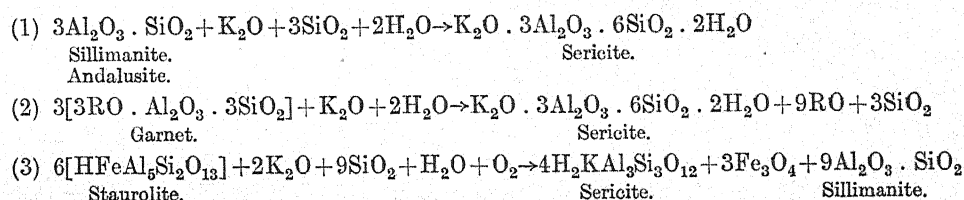
F. BECKE [10, pp. 134-40] has shown that myrmekite arises from a replacement of the potash in potash-felspars by soda and lime, and states that it is lacking in rocks with true igneous structures and was formed immediately after consolidation when the temperature was still near the consolidation temperature and solutions were active in the rock. J. J. SEDERHOLM [49, pp. 127-9] has shown that in addition to the origin given by BECKE, myrmekite may be formed during strong cataclastic metamorphism; C. E. TILLEY [50, pp. 88, 97-8] has recently described good examples of this metamorphic myrmekite.

In the Cromar rocks, the myrmekite appears all to belong to the true myrmekite of BECKE, and to result from the action of soda- and lime-bearing solutions. It is important to recall that the other Scottish rocks carrying conspicuous myrmekite—the Moor of Rannoch and the Lairg-Rogart granodiorites—recently described by the writer [43, p. 149; 44, p. 24;

45, p. 68] show a well-marked fluxional structure. The common occurrence of myrmekite in the Cromar rocks springing from the fine quartzo-felspathic layers may indicate that these acted as channels along which the solutions passed, producing during their passage a recrystallisation of the bands into the myrmekite-like association already described.

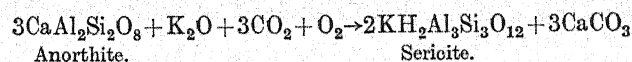
2. *Shimmer-aggregates*.—Thick coatings of fine-grained pale mica surrounding relics of the mineral replaced have been described and figured around andalusite, sillimanite, garnet, and staurolite, whether these minerals occur as probable xenocrysts or as parts of a xenolith. The shimmer-aggregates are so constant a feature of these rocks, and are so well developed, that it appears unlikely that they result from weathering processes. My friend, Mr A. G. MacGREGOR, who is studying the contact-metamorphism around the Lochnagar Granite, kindly permits me to state that he finds the shimmer-aggregates around minerals of the country-rock to be contact-altered by that granite. Thus, the formation of the shimmer-aggregates in these cases preceded the intrusion of the Younger Granite (see p. 348). Similar phenomena, though searched for, were not observed at the contact of the Biotitic Complex of Cromar against the Younger Granites of Coull and Tomnaverie, but this contact is not well exposed. It appears reasonable to regard the production of shimmer-aggregates as part of the injection-process.

The formation of white mica from the minerals concerned depends fundamentally on the accession of potash. Assuming that the white mica is muscovite, we may represent the changes as follows:—



In the last case, the sillimanite may be changed to sericite by a further access of potash, silica, and water; it will be recalled that the staurolite (fig. 5A) appears to fray out into a mass of sillimanite and this into sericitic micas.

Related to these phenomena may be the formation of albite by the destruction of anorthite, as in the much-shimmered xenoliths described on p. 330, thus:—



It has been repeatedly stated in the description of the Biotitic Complex that the feldspars are often partly sericitised; it is possible that this sericitisation is another aspect of the action of the potash-solutions responsible for the shimmer-aggregates.

In the formation of myrmekite, potash is released and is then available for the production of white micas. The amount of shimmer-aggregate is, however, far too great compared with that of myrmekite for such an origin of the potash to be at all likely. There are no indications as to the time-relations of myrmekite and the shimmer-aggregates, nor is there much evidence bearing on the date of the general sericitisation. The process probably occurred immediately after the consolidation of the injected material.

In summary, then, it may be stated that the post-consolidation action in the Biotitic Complex consisted of the disengagement of dominantly alkaline solutions, the soda (with lime) of which are responsible for the production of myrmekite, and the potash for the extensive sericitisation.



6. *The Pegmatites.*

In the description of the field-occurrence of the Biotitic Complex mention was made of certain thick straight-edged pegmatites, which traverse the complex, especially on Tomachalich and Craig Ferrar. Similar pegmatites are found in the quartzite and mica-schist belt of the Queen's Hill ridge. For reasons which will be advanced later (p. 348), these pegmatites are believed to be connected with the injection-phase rather than with the igneous period entirely later than the movements.

The oligoclase-biotite-gneiss and its associated rocks pass, as has already been described in their field-occurrence, into coarse patchy leucocratic varieties of pegmatitic character. These pegmatitic forms are part and parcel of the gneiss, being composed of the same essential minerals and carrying locally much garnet and sillimanite. They will not be further considered here.

The great transgressive pegmatites are all of one general type—potash-pegmatites. Their component minerals are quartz, potash-felspars, and muscovite. The perfectly fresh felspars comprise microcline, orthoclase, microcline-microperthite, and microperthite. Pale mica is variable in amount; often it forms large "books" of plates whose size may exceed an inch across.

The most salic stage of the injection is represented by countless quartz veins of all sizes found throughout the complex.

ORIGIN AND AFFINITIES OF THE OLIGOCLASE-BIOTITE-GNEISS.—The intrinsic character of the rock in the field indicates that the oligoclase-biotite-gneiss is primarily of igneous nature; but certain considerations, such as the chemical and mineralogical composition and the broader field-relations, lead to the conclusion that admixture with sedimentary material may have resulted in marked modification of the original magma. This question of the dual parentage of the oligoclase-biotite-gneiss is discussed in what follows.

There is abundant evidence of the magmatic behaviour of the oligoclase-biotite-gneiss. For instance, diversely oriented xenoliths of many rock-types swim in the gneiss which, on the other hand, veins and injects the larger sedimentary enclosures. But whilst in many cases it is an easy matter to decide where the magmatic rock ends and the sedimentary xenoliths begin, yet this is not always so. The soaked xenoliths and those of oligoclase-porphyroblast-schist pass imperceptibly into the oligoclase-biotite-gneiss; a similar gradual passage on a grander scale is provided by that of oligoclase-porphyroblast-schist into oligoclase-biotite-gneiss on Craigie (p. 322).

The extremely high normative corundum of the Dinnet oligoclase-biotite-gneisses (see p. 329) may be accounted for to some extent by the abundant colourless mica of the shimmer-aggregates which, it might be argued, may be due to weathering. Even if this sericitisation be taken as quite unconnected with the injection-processes, the abnormality in chemical composition of the undecomposed rocks is certainly not less than that of those analysed, for, in most cases, the alleged secondary mica will have replaced minerals with a far higher alumina-content than theoretical muscovite. The abnormal character of the Dinnet oligoclase-biotite-gneisses finds expression in the abundance of biotite and the absence of potash-felspar and the occurrence of garnet and sillimanite. It is instructive to compare the analyses (I and II of Table B, p. 329) with that (Analysis C) of an actual mixed rock from the Erzgebirge, consisting, according to C. GÄBERT [22, p. 353], of fine igneous stripes threading an aluminous hornfels. GÄBERT shows that the Analysis C can be exactly reproduced by mixing 1 part of



the analysed hornfels (corresponding to a "clayey greywacke") with  $5\frac{1}{2}$  parts of the analysed augen granite (corresponding to a biotite-granite). The analyses of GÄBERT's mixed rock and the Dinnet oligoclase-biotite-gneisses are thoroughly alike; potash is somewhat higher in GÄBERT's rock, a fact not without significance (see below). O. A. BROCH [11, pp. 90, 97-9, 141], in connection with the "basic gneiss-granite" of Nesodden, Oslo, an analyses (B) of which is given in Table B, remarks that this rock (exactly like the Dinnet oligoclase-biotite-gneiss in mineral composition) is transitional on the one hand to migmatites and on the other to granite-gneiss, and he considers it to be in part of syntectic origin. This mode of occurrence, intermediate in position between migmatites, plagioclase-porphyroblast-schists or leptynolites on the one side and a "granite" on the other, is shared also by the "granite surmicacé" of the French contacts described more particularly by A. LACROIX [33, II, pp. 36, 64]. The granite surmicacé is exactly like the Dinnet oligoclase-biotite-gneiss; the analysis (A) of a comparable mica-rich granitic rock from the celebrated Flamanville complex is given in Table B. The abnormal amount of biotite in these rocks is considered by LACROIX [33, II, p. 28] and the French school to be due to the endomorphic modification of the granitic magma by the assimilation of sedimentary schist. Again, C. N. FENNER [19, p. 602] for certain New Jersey granitic gneisses holds that the dark minerals of the country-rock have been taken up by the invading magma and recrystallised in large blades.

Such comparisons, combined with the chemical, mineralogical, and field-evidence already given in regard to the Dinnet oligoclase-biotite-gneiss, lead to the interpretation of this rock as of mixed origin. The sedimentary parent belongs to the quartzite and mica-schist group; the well-established greater resistance of siliceous rocks to "granitisation"—probably shown at Dinnet by the greater abundance and larger size of the quartzite xenoliths—permits of the conclusion that the more pelitic bands of the sedimentary country-rock play the dominant part. To establish the nature of the original igneous component is a question of some difficulty. There have been described on p. 323 injection-rocks consisting of igneous and sedimentary bands; such definitely mixed rocks pass, as a whole, into a homogeneous oligoclase-biotite-gneiss. It seems reasonable to regard the igneous bands of the mixed rocks as a fairly close approximation to the original igneous material which, by more complete mixture with the sedimentary bands, is modified to give oligoclase-biotite-gneiss. The igneous bands in question consist of quartz and oligoclase with variable and scarcer biotite; they have the characters of trondhjemites \* or trondhjemite-aplites as described by V. M. GOLDSCHMIDT [26] from the Stavanger region.

The chief constituents of the type trondhjemite [26, p. 79] of Dragaasen, Guldalen, Norway, are given in the table, p. 336. Next to them appears the average phyllite of the Stavanger region [24, p. 58].

The percentage composition of a mixture of equal parts of trondhjemite and the average phyllite can be compared with those of the Dinnet oligoclase-biotite-gneisses; the main discrepancies are in ferrous oxide and soda, but V. M. GOLDSCHMIDT [26, p. 85] gives analyses of many West Norwegian trondhjemites which are somewhat lower in soda than the rock used here. The employment of such a table as that on p. 336 means nothing more than that the origin of the Dinnet oligoclase-biotite-gneisses by the mixture of pelitic rocks and trondhjemitic

\* Trondhjemite is defined by V. M. GOLDSCHMIDT [26, p. 77] as follows:—"A leucocratic acid plutonic rock whose most essential light components are soda-rich plagioclase (oligoclase to andesine) and quartz, whilst potash-felspar is either absent or very subordinated. Amongst the mostly scanty, often very scanty, dark minerals biotite is the most important; the place of a small proportion of the biotite is often taken up by hornblende or, though more rarely, by a diopsidic pyroxene."

magma is not chemically impossible. GOLDSCHMIDT has briefly described [24, pp. 106-7, Pl. XIV, figs. 1 and 2] oligoclase-biotite-gneisses from the Stavanger region which are similar to those of Dinnet, but considers that there is as yet insufficient data as to their origin.

	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	FeO	MgO	CaO	Na <sub>2</sub> O	K <sub>2</sub> O
A. Trondhjemite . . . .	69.30	16.81	0.28	1.26	1.08	3.34	6.00	1.39
B. Average Phyllite . . . .	58.32	20.00	2.01	4.98	1.85	0.66	1.26	4.49
Mean of A. and B. . . . .	63.81	18.40	1.14	3.12	1.46	2.00	3.63	2.94
Dinnet oligoclase-biotite-gneisses . . . .	63.24 66.30	17.27 16.36	1.50 0.77	6.56 6.12	2.00 1.84	2.02 1.90	2.43 2.29	2.15 2.58

The question now arises as to how far the union of the igneous and sedimentary components of the oligoclase-biotite-gneiss is mechanical or chemical, that is, whether the materials of the invaded rock are xenocrystic in the trondhjemite magma or whether the oligoclase-biotite-gneiss results from the crystallisation of a magma modified by solution of the country-rock; in this latter event, the resulting products are contaminated rocks,\* according to the writer's definition of these [41, p. 128]. From the microscopic evidence there is no doubt that the oligoclase, biotite, and quartz of these rocks are crystallisations from the modified magma; the resulting rock is much richer in biotite than the original injection of probably trondhjemitic character; true sedimentary material can be recognised (p. 327), and is quite different from the oligoclase-biotite-gneiss proper. The status of the sillimanite and garnet is a question on which but little evidence is forthcoming. Sillimanite (p. 327) occurs almost entirely as large crystals with shimmer-aggregates—such crystals are possibly best interpreted as xenocrysts. The large unshimmered garnets are possibly of magmatic origin, whilst the fragmented “shimmered” crystals are xenocrystic. Some of the small patches extremely rich in “shimmered” garnet and sillimanite and chloritised biotite (such as are illustrated in fig. 4, p. 327) may represent spots of xenolithic sedimentary material. The impression is clearly formed in the field that the large sporadic garnets of the coarser, more variable, and often patchily pegmatitic form of the oligoclase-biotite-gneiss are of magmatic formation. The occurrence of garnet as a primary crystallisation in a granitic rock denotes, according to J. J. SEDERHOLM, A. OSANN, P. ESKOLA [17, pp. 30-1], and others, an excess of alumina in the magma—an excess thought by ESKOLA and SEDERHOLM, for instance, to be due possibly to the assimilation of sedimentary rocks. It is noteworthy that V. M. GOLDSCHMIDT [24, pp. 23, 26] believes that the occurrence of garnet and much biotite in the Stavanger trondhjemites near their contact with mica-schist is due to the derivation by the igneous rocks of material from the schists. H. SCHWENKEL [47, p. 196], in discussing the granite-gneisses of the Black Forest, pointed out, however, that garnet and sillimanite may arise by the combination of biotite and quartz.

3 Biotite + 4 Quartz → 2 Almandine + Sillimanite + 3 Orthoclase + Water.

\* The term *contaminated*, proposed in 1921, has been very widely adopted, but rarely with the narrow definition originally given. As now generally used, *contaminated rock* is equivalent to *Mischgesteine*, and includes all kinds of mixtures, both mechanical and chemical, of igneous rocks and country-rocks. It appears to the writer to be of little use striving against this extended definition, since the speed with which it has been adopted shows that some such English term was needed. In this now usual, more extended, sense, the Cromar oligoclase-biotite-gneiss is a contaminated rock whether the union of the igneous and sedimentary parts be purely mechanical or chemical.



Likewise, C. E. TILLEY [50, pp. 93-4] states that the garnet in certain South Australian gneisses is a normal pyrogenetic mineral due to the rearrangement of the biotite molecule, and is not a product of the absorption of aluminous sediments by the magma; the low-grade biotite and quartz passing to high-grade garnet, orthoclase, and water.

At Cromar, however, the field-evidence shows the intimate admixture of pelitic sediment and igneous material; the composition of the oligoclase-biotite-gneiss shows an alumina excess not all to be accounted for by xenocrystic sillimanite or late sericite; and these rocks, even when richly garnetiferous, contain little or no potash-felspar. It seems reasonable, therefore, to consider that part of the garnet of these rocks is a magmatic crystallisation due to the modification of the original magma by sedimentary material.

The oligoclase-biotite-gneiss shows everywhere a gneissose structure often combined with a mineral banding. There is no evidence for the cataclastic deformation of an already solid rock. The gneissic structures appear to be due to flow in a partly crystallised magma, and are emphasised by relics or ghosts of incorporated sedimentary material, and by the generally concordant lie of the xenolithic matter (see after, p. 346).

For many pages it has been apparent to the reader familiar with the researches of G. BARROW in the South-east Highlands that a great similarity exists between the Cromar oligoclase-biotite-gneisses and part of that worker's "Older Granite." A summary of BARROW's work is given in F. H. HATCH and A. K. WELLS' *Petrology of the Igneous Rocks*, 8th edit., 1926, pp. 427-31. In many publications BARROW has described oligoclase-biotite-gneisses, especially notable being those of Glen Muick and Glen Doll—nearest the Cromar area; these gneisses appear to differ in no respects, either petrographical or geological, from the Cromar rocks. The "Older Granite" is made up of a number of fractions resulting "from the progressive squeezing out of the liquid portion of granitic magma consolidating under stress. Each portion is slightly abnormal in composition, but were all parts mingled, the whole would make up a granite of normal composition." (HATCH and WELLS, *loc. cit.*, p. 430.) The petrographic types of the "Older Granite" fall into two groups, the alkali-granite type and the granodiorite type, the latter including the oligoclase-biotite-gneisses. Going south-eastwards from the oligoclase-biotite-gneisses of Upper Glen Clova, BARROW [4] found an increase of muscovite and microcline as against biotite and oligoclase, due to the straining off of potash-rich material towards the south-east. Thus, BARROW [3] interprets the oligoclase-biotite-gneiss as the first crystallisation from a granite magma, the liquid potash-rich residuum having been expelled.

This present paper contains the results of a detailed study of a small area; these results apply only to that area and cannot be used in criticism of those gained by BARROW in a much wider sphere. However, the comparison of the origin of the Cromar gneisses given in this paper and that of the South-east Highland oligoclase-gneisses advanced by BARROW may be worth making:—

1. For Cromar, the oligoclase-biotite-gneiss is thought to result from the admixture, both chemical and mechanical, of a trondhjemitic (oligoclase-quartz) magma and dominantly pelitic sediment.

2. For the South-east Highlands, the oligoclase-biotite-gneisses are considered by G. BARROW to result from the expulsion of potash-rich material from a granitic magma.

It may, however, be mentioned that the presence of kyanite, sillimanite, andalusite, and cordierite in the oligoclase-biotite-gneiss of several localities suggested to BARROW [6, p. 50; 7, p. 98; 8, pp. 67, 68] the possibility of the absorption of shaly material. The Cromar oligoclase-biotite-gneisses appear to be identical with the oligoclase-biotite-gneisses of Glen



Muick and Glen Doll, as described by BARROW. In their mode of origin suggested here, however, they resemble another part of that author's "Older Granite," namely the *Duchray Hill Gneiss*. This rock, alternatively called the "oligoclase-muscovite-biotite gneiss," was recognised by J. J. H. TEALL as of mixed sedimentary and igneous origin. The descriptions provided by BARROW [7, pp. 101-2; 8, pp. 69-70] stress the presence of large six-sided crystals of muscovite in this rock. It seems possible that BARROW has over-emphasised the importance of muscovite in the Duchray Hill gneiss and that the Duchray Hill and Cromar gneisses are thoroughly similar. Indeed, it may be that the two origins given above for the oligoclase-biotite-gneisses are not necessarily mutually incompatible. In the richly garnetiferous and sillimanite-bearing gneiss of Cromar we may have on a larger scale phenomena which are reproduced, except for the Duchray Hill area, in only small portions of the oligoclase-biotite-gneiss of the South-east Highlands. Much detailed work is necessary on the "Older Granites" before these points can be properly elucidated; it will perhaps be helpful at present to refer to the oligoclase-biotite-gneiss of Cromar always with the place-name attached.

#### APPENDIX TO THE BIOTITIC COMPLEX.

##### *Oligoclase-porphyroblast-schists.*

*Field Occurrence.*—Mica-schists, showing conspicuous porphyroblasts of oligoclase, have a wide distribution in Cromar (see fig. 1, p. 318). They are best seen about Dinnet at the following localities: (1) excellently in crags at Dinnet House; (2) in the woods between Lochs Davan and Kinord; (3) on the north bank of the Dinnet Burn,  $\frac{1}{4}$  mile above Mill of Dinnet; and (4) on Mulloch. Similar porphyroblastic schists are found on Balnagowan Hill. In addition to these broader outcrops, they occur as narrow belts or bands throughout the complex. Everywhere their strike and dip are in accord with those of the adjacent country-rocks. Associated with the main bodies of these schists are siliceous beds and belts of mica-schist.

The marginal relations of these oligoclase-porphyroblast-schists are of importance. On Balnagowan Hill there is a gradual increase in the number of porphyroblasts northwards, providing a good transition from the purely sedimentary schists of the Queen's Hill belt into the definitely magmatic rocks to the north. Again, on Mulloch and Craigie the oligoclase-porphyroblast-schists pass gradually eastwards into definite xenolithic injection-rocks (see p. 322). Their western extension beyond Dinnet is not yet known. I have encountered them, however, on the east side of Glen Muick where it is possible that their origin may be finally settled.

In the field, these rocks resemble coarse feldspathic grits. They are homogeneous and never contain inclusions of other rocks; over practically the whole of their outcrop they show no patently intrusive igneous material apart from a few potash-pegmatite veins.

*Petrography.*—The oligoclase-porphyroblast-schists are dark grey in colour and show white feldspar crystals, lenticular in form, wrapped about by biotite-rich streaks. The feldspar crystals usually conform with the structure lines of the rock, but occasionally they lie athwart these. They reach half an inch in size and are sometimes clustered together into nests or patches, as on Mulloch. In slice (fig. 3A, p. 325), the rock is seen to be composed of feldspar, quartz, and biotite with accessory garnet, zircon, and muscovite. The feldspar occurs in large rounded grains showing quite undistorted twin-lamellæ; in composition it varies from  $Ab_{80}An_{20}$  to  $Ab_{75}An_{25}$ ; it encloses small quartz grains, garnets, and plates of biotite. Quartz forms areas of small grains or occasionally large isolated grains. Biotite, with a pale yellow,  $b=c$  clear

deep brown with a red tinge, occurs as small laths, either aggregated or scattered in trains through the quartz areas. As regards structure, the rock is made up of a base of tiny quartz grains and biotite flakes which flow around larger quartz grains and rounded feldspars, some of these being of large size. Eye-shaped areas of aplitic substance are rare. There is no sign of cataclasis. The base of the rock often shows the hornfels-structure of contact rocks of Christiania type. In the slices examined, large *garnets* are sporadic: these are fractured and separated into pieces, the cracks being filled with quartz and biotite. The heavy residue from a crush of the oligoclase-porphyroblast-schist whose analysis is given below showed abundant garnet.

The analysis of a typical oligoclase-porphyroblast-schist from the north face of Mulloch is given as Analysis I in Table C below:—

TABLE C.  
*Plagioclase-porphyroblast-schists, etc.*

	I.	A.	B.	C.	D.	E.
SiO <sub>2</sub>	68.70	64.70	66.36	63.4	65.11	60.95
Al <sub>2</sub> O <sub>3</sub>	13.63	15.45	15.81	18.1	15.78	16.00
Fe <sub>2</sub> O <sub>3</sub>	1.29	1.36	0.77	6.7	} 6.49	4.37
FeO	4.11	4.18	4.12	..		..
MgO	1.75	1.48	1.87	1.9		2.97
CaO	3.04	2.92	2.15	0.9	1.34	3.02
Na <sub>2</sub> O	2.72	3.09	2.49	3.2	2.49	2.93
K <sub>2</sub> O	2.00	3.46	3.63	3.2	3.97	2.40
H <sub>2</sub> O+	1.34	1.82	1.67	} 2.8	} 1.41	1.62
H <sub>2</sub> O—	0.70	0.15	..			0.34
CO <sub>2</sub>	nil	0.85	..			0.09
TiO <sub>2</sub>	0.42	0.59	0.81	trace	0.83	1.17
P <sub>2</sub> O <sub>5</sub>	0.09	0.19	0.33	..	0.25	0.12
S	trace	0.05	..	..	0.14	(FeS <sub>2</sub> 2.57)
MnO	0.07	0.05	..	..	0.24	0.21
BaO	..	0.10	..	..	..	0.03
C	..	..	..	..	..	1.44
	99.86	100.44	100.01	100.2	100.39	100.23

I. *Oligoclase-porphyroblast-schist*, Mulloch, Dinnet, Aberdeenshire. *Anal.*, W. H. HERDSMAN.

A. *Albite-porphyroblast-schist*, Stavanger, Norway. *Anal.*, O. RÖER [in 24, p. 84].

B. *Garnet- and amphibole-bearing quartz-muscovite-biotite-schist*. *Contact-schist* of A. GAVELIN, Kvikkjokk, Sweden. *Anal.*, R. MAUZELIUS [in 23, p. 323]. *Albite-porphyroblast-schist with garnet and amphibole* of V. M. GOLDSCHMIDT [24, p. 127].

C. *Albite-schist*, Stuck Burn, Cowal. *Anal.*, J. J. H. TEALL [in 12, p. 39].

D. *Albite-gneiss*, Rudha Ban, Loch Lomond. *Anal.*, W. POLLARD [in 15, p. 23].

E. *Black Schist*, Sandend Harbour, Banffshire. *Anal.*, E. G. RADLEY [in 41, p. 64].

ORIGIN AND AFFINITIES OF THE OLIGOCLASE-PORPHYROBLAST-SCHISTS.—There are two groups of rocks in the Caledonian mountain-chain with which the Cromar oligoclase-porphyroblast-schists show marked mineralogical or chemical affinities. These two groups are on the one hand, the albite-schists of Cowal and Loch Lomond in Scotland, and on the other, the albite-porphyroblast-schists of Scandinavia. Quite different explanations have been advanced for the origins of these two groups by petrologists who have studied them. The Scottish albite-schists are considered to be normal metamorphic sediments in which



introduction of material from without has played no part; the Scandinavian albite-porphyroblast-schists are regarded as due to the immigration of silica, soda, and lime into a normal potash-dominant phyllite. It is intended here in the first place to compare the Cromar rocks with both of the groups just cited, and then to consider from the evidence available their possible genesis.

The albite-schists of Cowal were described by Sir J. J. H. TEALL and C. T. CLOUGH [12, pp. 39-45, 297, 299]. CLOUGH, probably influenced by an unfortunate choice of material for comparative analysis (*cf.* E. B. BAILEY [2, p. 325]), suggested the possibility of an impregnation of soda in their production [12, p. 39]. On the other hand, E. H. CUNNINGHAM CRAIG [15] in describing the albite-schists and gneisses of the Loch Lomond district considered that these rocks could be produced by the metamorphism of greywackes without transfer of material. The origin of the Scottish albite-schists has been recently discussed by E. B. BAILEY [2, pp. 323-5], who concludes that "the albite-schists and gneisses of the South-west Highlands have resulted from metamorphism of greywacke-shales; and that, though migration of material has certainly occurred, it is only on a small scale and of a strictly intra-formational character" [2, p. 325].

The albite-schists of the South-west Highlands and the oligoclase-porphyroblast-schists of Cromar are associated with rocks of quite different metamorphic grades; there is little advantage in comparing the details of microscopic structure in the two classes. What is of more importance is to inquire whether there are purely sedimentary schists of a composition reasonably similar to that of the albite-schists and oligoclase-porphyroblast-schists. In Table C, p. 339, two analyses (C, D) are given of Scottish albite-schists and gneisses. These may be compared with that of the Cromar oligoclase-porphyroblast-schist. There is reasonable agreement except in the amount of lime and potash. E. B. BAILEY [2, p. 324] has shown "that a mixed series of greywacke and shale must be expected to contain some proportion of greywacke-shale of a composition corresponding with" the analyses of the albite-schists C and D of Table C. Similarly for the Cromar oligoclase-porphyroblast-schist, there is no doubt that the analysis could be reproduced by a mixture of greywacke and slightly calcareous phyllite. Except for the greater content of lime, the Cromar schist closely resembles certain "greywackes with dominant soda," listed by G. LINCK [35, p. 298]. Finally, attention may be directed to the analysis, E of Table C, of the Black Schist of Banffshire which shows a lime : soda : potash ratio quite similar to that of the Cromar rock.

Such comparisons as these indicate that the Cromar oligoclase-porphyroblast-schists have a chemical composition not radically different from rocks of purely sedimentary origin, and that they may result from the metamorphism of such sediments without the introduction of new material.

Turning now to the affinities between the Cromar rocks and felspar-porphyroblast-schists in whose origin transfer is considered to have operated, one finds the very closest similarities. The Cromar oligoclase-porphyroblast-schists agree in slice with the albite-porphyroblast-schists of Stavanger described and figured by V. M. GOLDSCHMIDT [24, pp. 81-2, and especially Pl. X, which should be compared with fig. 3A of this paper, showing the Cromar rock]. The main difference between the two schists is that in the Scandinavian rocks the porphyroblasts are mostly oligoclase-albite ( $Ab_{90}An_{10}$ ), varying from albite to oligoclase ( $An_{28}$ ), whilst in the Scottish rocks the dominant porphyroblast is more calcic, being  $Ab_{80}An_{20}$ - $Ab_{75}An_{25}$ . The chemical analyses of rocks from the two localities (Table C, Analyses I and A) show a marked similarity, the chief differences lying in the ratio of alkalies and in the amounts of potash. A comparable relation holds between the Cromar rock and those (Table C, Analysis



B) from Sweden described by P. QUENSEL [40, p. 19], and A. GAVELIN [23, p. 313], and discussed by V. M. GOLDSCHMIDT [24, pp. 126-8], who shows them to be identical with the Stavanger albite-porphyroblast-schists.

The Stavanger albite-porphyroblast-schists are restricted to a narrow zone around an intrusion of trondhjemite from which the material added to the original phyllite was drawn. From a long series of chemical analyses V. M. GOLDSCHMIDT [24, pp. 108-120] considers that there has been an absorption by the country-rock of silica, soda, and lime, the silica and soda being derived from the magma, the lime from non-magmatic solutions circulating in the contact-zone. Thus, GOLDSCHMIDT regards [24, p. 114] the albite-porphyroblast-schists as having arisen from the average Stavanger phyllite [24, p. 113] by the addition, to 100 parts of this, of 26 parts silica, 3.1 parts lime, 2.8 parts soda, and the withdrawal of 1.7 parts water.

E. B. BAILEY [2, p. 326] has drawn attention to certain aspects of GOLDSCHMIDT's work. He points out that the rocks analysed by the latter and used to give the results noted in the preceding paragraph come from different stratigraphical horizons and had not necessarily the same initial compositions. A further complexity is produced by the presence of numerous thrusts. Finally, however, BAILEY stresses the thoroughness of GOLDSCHMIDT's investigation and the apparent continuity in the various stages connecting phyllite with injection-rocks observed in the Stavanger region.

From the descriptions of the "leptynolites" (felspathised mica-schists) of A. LACROIX and the French School, it appears that rocks like the Cromar oligoclase-porphyroblast-schists play an important part in the celebrated granite contacts of the Pyrenees and other French localities [see especially 33, pp. 249-50, and Pl. I, figs. 2-4]. The purely mechanical mixing of felspathic material with country-rock is invoked in many cases by C. BARROIS, A. MICHEL-LEVY, and A. LACROIX for these contacts, but the general position of these petrologists is best indicated by the statement of LACROIX [33, p. 288].

"Les phénomènes de contact des roches éruptives sont le résultat de la transformation d'une roche préexistante, apportant sa caractéristique personnelle, sous l'influence d'agents minéralisateurs, le plus généralement accompagnés d'éléments volatils ou solubles qui, en se fixant sur la roche modifiée, en transforment plus ou moins complètement la composition chimique."

Lastly, oligoclase-porphyroblast-schists seem to occur in the Irish granite-complexes described by G. A. J. COLE [13, pp. 212-3, Pl. II, fig. 2; 14, pp. 184-5], but little detailed petrographical or chemical work has been done on these.

It has now been shown that rocks similar to the Cromar oligoclase-porphyroblast-schists occur in close connection with injection-complexes, and that in both Scandinavia and France it has been held that an important influx of material takes place in their formation.

Now that the similarities between the Cromar oligoclase-porphyroblast-schists and, on the one hand, the sedimentary albite-schists and, on the other, the injection-metamorphosed albite-porphyroblast-schists or leptynolites have been pointed out, the evidence concerning the origin of the Cromar rocks must be considered.

In the first place, the Cromar schists appear to take the place of the purely sedimentary schists lying above the Deeside Limestone. In the Queen's Hill belt of unmixed sediments there is no development of oligoclase-porphyroblast-schists, yet in the Dinnet area such schists are magnificently developed on exactly the same stratigraphical horizon. Secondly, the oligoclase-porphyroblast-schists of the Dinnet area pass, on Mulloch and Craigie, by a well-exposed transitional zone into xenolithic injection-rocks. This passage takes place along

the strike, whereas on Balnagowan Hill a similar passage is found at right angles to the strike. They are thus intimately associated with injection-phenomena. Thirdly, it has been considered probable (p. 335) that the igneous component of the injection-complexes was of a soda-rich trondhjemitic character, so that the juxtaposition of soda-rich igneous rocks with soda-rich alleged sedimentary rocks is remarkable if this association is purely fortuitous. The Cromar oligoclase-porphyroblast-schists appear, therefore, to be reasonably interpreted as genetically connected with injection-processes.

In the *Geological Survey Memoir*, on Sheet 76 [29, p. 11] of 1890, the oligoclase-porphyroblast-schist of Mulloch was considered to be a grit, the porphyroblasts being taken as pebbles. That such an explanation is unlikely is shown by the inclusion of biotite, quartz, and garnet in the porphyroblastic feldspars.

If it be admitted that the Cromar oligoclase-porphyroblast-schists arise by injection-metamorphism, it is necessary to discuss how far the new feldspars set up in them derived their material from the magmatic fluids or from the country-rock itself. This question can be answered only by chemical analyses of the same band of rock within and without the zone under consideration. Such a chemical investigation was impossible at Cromar, nor has it been done in any of the injection-complexes yet studied. Certain loose results derived from the general data available may, however, be of interest.

Neglecting the possibility that the original rock of the Dinnet schists was initially soda-rich, one finds that analyses of unmixed pelitic and semipelitic sediments of the Dalradian Series [*e.g.* 41, p. 64] indicate in general that such sediments, when compared with the Dinnet oligoclase-porphyroblast-schists, show (1) considerably more alumina, and (2) a reversal of the alkali-ratio, potash being dominant, and usually markedly so, in the normal sediments. Such sediments are seen to be of the same general chemical type as the average Scandinavian phyllite employed by GOLDSCHMIDT [24, p. 113] as the initial rock of his albite-porphyroblast-schists. The results of GOLDSCHMIDT's operations have already been given on p. 341. A good chemical balance with the Cromar oligoclase-porphyroblast-schists is produced by adding, to 100 parts of GOLDSCHMIDT's initial sediment, 45 parts silica, 4 parts lime, and 3 parts soda, and taking away 2 parts of water. It may be suggested, then, that in the formation of the oligoclase-porphyroblast-schists there has been a transfer from magma to country-rock, and that the material transferred is a soda-lime-silicate free from or poor in alumina. Such a silicate, combining with alumina of the sediment, produces feldspathisation. At all events, acid plagioclase-feldspathic, aplitic, pegmatitic, granitic, trondhjemitic or granodioritic materials are all too rich in alumina or potash to be the transferred substances, provided, of course, that the assumption that the original rock was a potash-dominant sediment is valid.

Which of the two interpretations of the Cromar oligoclase-porphyroblast-schists just discussed proves to be correct depends upon further research on similar rocks in the Scottish complexes. It is necessary, therefore, once more to emphasise the tentative nature of the conclusions put forward and to recall that, though the oligoclase-porphyroblast-schists are included with the injection-complex in fig. 1, their true nature is yet to be clearly proved.

#### B. THE HORNBLENDIC COMPLEX.

The injection-phenomena in which the host is igneous rock of the Greenstone Series may be considered in two zones or belts:—

1. Pegmatised Hornblende-schists (Craig Dhu).
2. Hornblendic Complex (Tillyhermack).



1. *Pegmatised Hornblende-schists of Craig Dhu.*—This type of phenomena is found within the limits of the Biotitic Complex. It is especially well seen on the great rock-exposures forming the summit ridge of Craig Dhu: a good line of traverse starts on the south at the Blue Cairn and follows a fence running north by west over the summit and thence northwards to the targets at the north foot of the hill. Phenomena similar to those of Craig Dhu can be less well seen at several localities, as on Balnagowan Hill, at Balnacraig, and on the south slopes of Scar Hill.

The main part of Craig Dhu consists of massive fine-grained black hornblende-schists or hornblende-granulites, consisting of hornblende and labradorite; clinopyroxene is seen in certain bands. These hornblendic rocks are veined with great blotches, patches, and strings of felspathic material (oligoclase) that is seen to isolate and incorporate the hornblende of the invaded rock. Transverse veins spread out laterally into patches and become hornblendic, but lit-par-lit injection is only occasionally seen. When the host is garnetiferous, the hornblende-pegmatites traversing it are likewise garnetiferous. Immediately adjacent to the injections the hornblendes of the hornblende-schist or granulite are extremely large, a circumstance arising from mineraliser-action. An interesting example of similar action is provided by a trail of enlarged hornblendes winding away from the seen termination of a hornblende-pegmatite; here mineralisers have penetrated farther through the rock than the felspathic material; the phenomenon recalls C. BARROIS' classic example of felspar trails in the Ros-trenen granite contacts. It is noteworthy that the hornblende occurring in the pegmatites consists of very large, usually isolated, crystals, a case presumably of the same type of mineraliser-action.

The occurrence of hornblende in pegmatites traversing hornblendic rocks has been noted by many observers, *e.g.* by J. J. SEDERHOLM [48, p. 109] and P. ESKOLA [17, pp. 58, 60] in Finnish contacts, V. M. GOLDSCHMIDT [24, p. 54] in the Stavanger region, P. NIGGLI [27, p. 327; 37, p. 169] in the Alps, F. REINHOLD [46, p. 145] in Austria, G. KLEMM [32, p. 15], and H. PHILIPP [38, p. 77] in Germany, and by C. E. TILLEY [50, pp. 83, 88, 90] in South Australia. In all cases, the hornblende is considered to have been derived from the hornblendic country-rock. Similarly, the enlargement of hornblende adjacent to veins occurs in many complexes as noted by H. SCHWENKEL [47, p. 167, Pl. IV, fig. 5], F. REINHOLD [46, pp. 86, 90, 99], H. PHILIPP [39, pp. 404-6], W. FEHR [18, pp. 336-7], and P. NIGGLI [27, pp. 326-7, 359; 37, p. 169].

Traversing the hornblende-granulites of Craig Dhu are certain very large, straight-edged, coarse pegmatites that presumably represent the same phase of the complex as those described on p. 334 from the Biotitic Complex.

Perhaps half of Craig Dhu is made of pegmatised hornblende-schists and granulites, whilst the other half consists of bands of varying width of oligoclase-biotite-gneiss and lit-par-lit injection-complexes with siliceous and pelitic rocks. Whilst the sedimentary rocks have been mechanically and chemically incorporated in the injected magma, the old igneous rocks have simply been veined by pegmatitic material; to find the hornblendic complex in the same stage as the biotitic complex of Craig Dhu one must go to the Tillyhermack region, north of the Biotitic Complex. Craig Dhu illustrates a marked feature of the Cromar Complex, namely, the resistance to injection and complexing shown by the rocks of the Greenstone Series as compared with the sedimentary country-rocks.

2. *Hornblendic Complex of Tillyhermack.*—It has already been noted (p. 322) on the traverse along the fence from Scar Hill to Tillyhermack that the oligoclase-biotite-gneiss gives place northwards to a hornblendic complex (see fig. 1, p. 318). From the locality of



this change, the Hornblendic Complex is well exposed for one-third of a mile to Tillyhermack, where are a large quarry and bold crags; good exposures are also seen on the south face of a ridge running eastwards from the quarry.

These exposures reveal a coarse fluxional or gneissic variable hornblendic and hornblende-biotite rock; it is patchy; unsoaked xenoliths are abundant and are all of black fine-grained hornblende-schist; diversely oriented enclaves in non-foliated hornblendic complex are repeatedly seen. The dominant acid hornblendic complex encloses nebulitic patches or clearer xenoliths of more basic hornblendic material, whilst patches of basic complex hold enclaves still more basic. There are many fairly homogeneous areas of intermediate rock resembling a lamprophyre and weathering pinkish. Some varieties of the hornblendic complex show large acicular hornblendes. Pegmatites in veins and patches are abundant: these are often hornblendic and pass imperceptibly into the hornblendic complex. In Tillyhermack Quarry, the very variable patchy and veined complex is dominantly hornblendic; it is traversed by biotite-pegmatites.

On the south-west face of Tomachallich there is a patch of hornblendic complex like that of Tillyhermack. An acid hornblendic rock contains large unoriented enclaves of more basic material, all traversed by thin feldspathic veins.

*Petrography.*—In slice (fig. 6A) the coarse, streaky, or fluxional hornblendic rock—*pseudodiorite*—shows large plates of hornblende as the dominant component, with a pale yellow, to green-brown, to greenish blue; it is slightly sieved and occasionally twinned. Feldspar, in the main oligoclase-andesine, but varying slightly on either side, forms large lensed crystals, sometimes showing patches of minute sericitic material. Quartz occurs in patches of grains. Biotite, with a queer bleached or washed-out colouration, forms ragged collections of shreds; often it appears to occur along certain channels in the rock. Apatite, sphene, zircon, and orthite are accessory. In some slices, there is very little quartz, whilst in others biotite is fairly abundant. In these rocks, areas or streaks of finer-grained hornblende feldspar and biotite occur; these presumably represent reconstructed xenoliths. Whilst usually the structure is gneissic, some rocks show no particular orientation of their components.

The *pseudo-lamprophyric* type (fig. 6B) already mentioned is of widespread occurrence as patches in the complex. In slice, it shows small prisms of hornblende, bleached, or chloritised ragged laths of biotite, xenomorphic interstitial quartz and euhedral feldspar; the latter is zoned, and when determinable, seems to vary from oligoclase (about  $An_{20}$ ) to more sodic types near albite; these crystals show a slight sericitisation. Apatite and sphene are abundant accessories. The rock in structure is strikingly like some of the Odenwald malachites. Occasionally porphyritic crystals of feldspar and hornblende are seen. These rocks sometimes show a good crystal-orientation.

Other types of hornblendic complex show euhedral hornblende and biotite in very large feldspar plates; plagioclase is by far the dominant feldspar. The biotite is bleached, the feldspar slightly sericitised and the hornblende shows a fibrous alteration at its margins and along its cleavages.

The basic hornblendic rocks that occur *xenolithic* in the more acid types just described are seen in slice to be composed of euhedral hornblendes and large biotites enclosed in large subhedral crystals of oligoclase (about  $An_{20}$ ). Sphene and apatite are abundant: quartz is interstitial. The biotite is bleached, ragged, and split; ore-dust is collected along its cleavages and around its edges. The feldspar shows slight sericitisation; in some slices epidote is abundant in the feldspar. Mafic components often form half of these rocks.

A slice from Tomachallich shows albite-oligoclase with twinning of checker-type; the

hornblende is colour-banded by growth stages; irregular later growths have taken place about the euhedral central crystals so that the old scattered prisms become joined up into large shapeless plates. Further diminution in the amount of salic components leads to a type of xenolith found on Tomachallich and around Tillyhermack. In hand-specimen it is a coarse-grained scyelitic-looking rock; in slice it is seen to be composed entirely of hornblende in very large plates formed by fresh growth from isolated prisms (fig. 6C).

Hornblende *injection-gneisses* from these complexes show bands and lenses of large

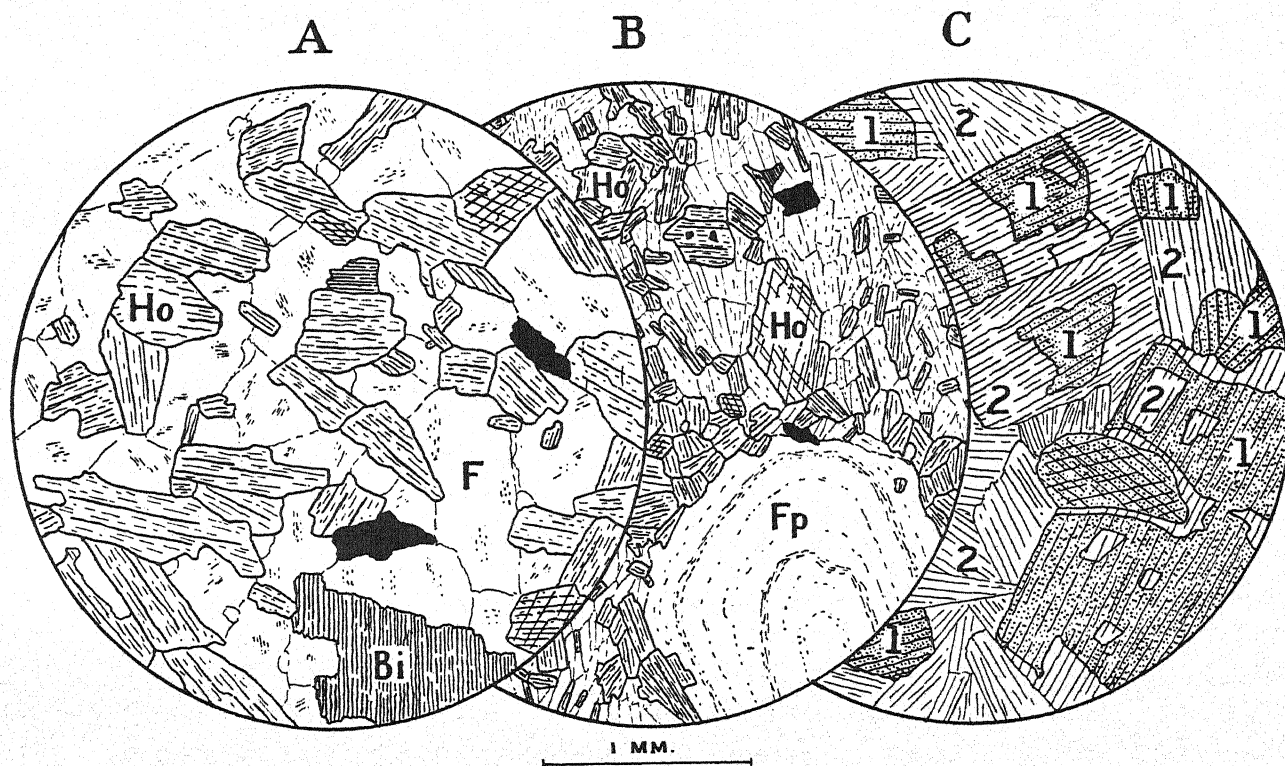


FIG. 6.—Rocks of the Hornblende Complex.

- A. Pseudo-dioritic Type. Ho = hornblende, F = plagioclase, Bi = biotite, solid black = iron-oxide.  
 B. Pseudo-lamprophyric Type. Ho = hornblende, Fp = porphyritic plagioclase, solid black = iron-oxide.  
 C. Hornblende Xenolith. 1 = brown hornblende, 2 = pale green hornblende.

oligoclase crystals between fine-grained quartz-felspar-biotite-hornblende streaks, with occasional very large hornblendes in both.

**ORIGIN AND AFFINITIES OF THE HORNBLENDE COMPLEX.**—The pseudo-dioritic rocks of the Hornblende Complex are considered to result from the incorporation of basic igneous rocks of the Greenstone Series in an oligoclase-rich, possibly trondhjemitic, magma. Evidence bearing on this is contained in the description of the field and microscopic characters of the complex; a few aspects of this may be recalled.

In the pegmatized hornblende-schists and granulites, the first stage of the process believed to have operated is shown in the irregular veining by oligoclase-rich injections and in the hornblende rocks resulting from the patchiness of these. As should be expected, the injected material is seen to be the same as the igneous component of the Biotitic Complex.

In the pseudo-dioritic rocks of Tillyhermack there is supplied the more complete stage of the injection-processes, and in these the injected material and the older rock are more thoroughly mixed, yet one parent of the complex is revealed by the exclusively amphibolitic nature



of the xenoliths. Further, the lit-par-lit complexes, though rare, substantiate the conclusion, derived from the pegmatized hornblende-schists, that the igneous parent was oligoclase-rich. It seems possible that the hornblende of the pseudo-dioritic rocks results from the recrystallisation of the older hornblendes rather than from the absorption and deposition of these *de novo* from the magma. The richness of the Hornblendic Complex in biotite is an important point to which reference is made below.

The formation of pseudo-dioritic rocks by the incorporation of amphibolites in acid igneous injections has been favoured by several observers. From what appear to be hornblendic complexes exactly like that of Cromar, G. BARROW [6, p. 50; 7, pp. 97-8; 8, pp. 57-8] obtains "conclusive evidence of the absorption of epidiorite" [7, p. 98] with, in Glen Muick, the production of hornblendic gneisses of "Lewisian Gneiss Type." In the Finnish migmatite areas there are pseudo-dioritic rocks showing close resemblances to those of Cromar. Thus, in the Pelling region, J. J. SEDERHOLM [48, pp. 96, 109, 113-28] describes migmatites, resulting from the injection and incorporation of amphibolite by various granites, that are indistinguishable in SEDERHOLM's figures from the Cromar pseudo-diorites. In Sweden, A. G. HÖGBOM [30] finds very beautiful complexes of granite and diabase, in which intermediate rocks are formed by the melting and resorption of the earlier rock; one tablet on his map of Nordingrä is labelled "gabbro-granite." Again, in the Albtal granite, H. PHILIPP [39, p. 336] considers certain hornblendic varieties to arise by the resorption of amphibolite inclusions.

In the Hornblendic Complex there are many examples of the action of solutions, either gaseous or liquid, to which brief reference has already been made. The presence of biotite in the basic enclaves and in the reconstructed xenoliths, possibly indicates a transfer of potash into the original amphibolite. V. M. GOLDSCHMIDT [24, p. 54] has briefly stated that "metasomatische Prozesse dürften sich in Amphiboliten vorwiegend durch Biotitbildung äussern," whilst O. A. BROCH [11, pp. 133-4, 144-8] has described plagioclase-biotite-gneisses resulting from such a production of biotite in amphibolite. Similarly, F. REINHOLD [46, p. 145] found a biotite-rich zone in amphibolites at their contact with veins in the Waldviertel; O. H. ERDMANNSDORFER [16, p. 113] has assembled several cases of a similar transfer of potash.

The action of potash-bearing solutions is also evident in the Cromar rocks by the formation of ragged biotite along what appear to be channels in the rock, and by the general ragged aspect of the biotite plates in the Hornblendic Complex (*cf.* P. NIGGLI [27, p. 440]).

#### C. THE RELATION BETWEEN INJECTION AND METAMORPHISM.

One of the most important, and at the same time one of the most difficult, problems of the injection-complexes concerns their relation to the general metamorphism. The igneous intrusion responsible for the injection-complexes is undoubtedly part of G. BARROW's "Older Granite." The general outlines of BARROW's views on the relation of the Older Granite to the general metamorphism are well known. The country-rocks of the Cromar area lie, according to BARROW [9], within his sillimanite aureole; sillimanite "does not extend in width much beyond the area where the older granite material emerges in considerable quantity at the surface" [5, p. 23], and he considers it "reasonable to attribute both the minerals and the crystallisation to the thermometamorphism of the intrusion" [4, p. 337]. BARROW [*e.g.*, 8, p. 24] has considerably elaborated this simple statement, but for the discussion of the small Cromar area it is sufficient to consider the general idea.

The nature of the gneissic structure of the oligoclase-biotite-gneiss must be dealt with first. This structure is believed (p. 337) to result from flow in a partly crystallised magma containing relics of incorporated sedimentary material. The oligoclase-biotite-gneiss shows



no signs of cataclastic deformation and is quite different from the augen-gneisses of North-east Scotland, such as those of Boggierow (Portsoy) and Keith [41, pp. 101-2]; there is no trace of superposed metamorphism such as would be produced had an originally banded or oriented solid rock been subjected to later deep-seated stresses. Heterogeneity having been produced in the complex magma by the presence of xenolithic material and by the separation of a considerable body of crystals, the effects of stress could become apparent; the structure of the gneiss is thus formed. The Cromar injection took place under conditions of stress.

The character of the xenoliths in the oligoclase-biotite-gneiss must now be considered. These xenoliths are schistose; many cases have been cited in which adjacent xenoliths lie with their individual foliation-planes at all angles to one another; around these unoriented xenoliths the oligoclase-biotite-gneiss flows in sinuous curves. It has been shown that the oligoclase-biotite-gneiss cannot be interpreted as an originally fluxional rock sheared in the solid by later movements. Let us suppose it possible for a magma, intruded under stress, to pick up non-metamorphosed country-rock as xenoliths—non-crystalline xenoliths occurring scattered through the magma. Any pressure on these xenoliths would be hydrostatic; any contact-metamorphic effects produced in them would be of the Christiania or Barr-Andlau hornfels-type; they would show no directed structures. In such a case, the xenoliths would be of hornfelses and not of schists. Further, for Cromar, the non-uniformity of the direction of structures in adjacent xenoliths *inter se*, and in the surrounding gneiss as compared with the xenoliths, cannot be explained if the xenoliths were non-schistose at the time of their incorporation in the magma. It is reasonable to believe, therefore, that the xenoliths were already foliated when they became included in the magma.

Again, lit-par-lit injection is very beautifully developed over most of the oligoclase-biotite-gneiss area. This means that there were planes in the country-rock along which igneous material was able to penetrate. It is best to consider that these planes were foliation-planes rather than bedding-planes, say, in non-schistose sandy and clayey sediments.

Turning now to the consideration of the Hornblendic Complex, we find there the same evidence for the Greenstone Series being metamorphic schists before they were involved in the injection-complex. Though lit-par-lit injection is somewhat rare in the Hornblendic Complex yet it does occur, and injection must have followed planes that, in this case, can have been only those of foliation. Similarly, all directions of orientation of schistosity are found amongst the hornblende-schist xenoliths in the Hornblendic Complex.

There seems thus to be a considerable body of evidence in favour of the view that the siliceous and pelitic country-rocks and the Greenstone Series were already metamorphic when their xenoliths were taken up by the magma injected. Though this is so, it does not necessarily follow that the general metamorphism and the injection were widely separated in time. The injection may have occurred during the later stages of the movement-period whilst the high-grade metamorphism of the sillimanite aureole was most probably accomplished during the earlier stages of the same period. The sequence of events may have been somewhat as follows:—

(a) Folding in the geosyncline produced two main results—heating of the deeper beds and the ascent of the magmatic region. By this combination, the country-rocks were maintained for a lengthy period at a high temperature adjacent to a large body of possibly granodioritic magma and were also under powerful stresses—the result is seen in the sillimanite-gneisses, etc., of the country-rocks, and in the hornblende-schists and granulites of the Greenstone Series. This is the *General Metamorphic Period*.

(b) Towards the close of the movement-period crystallisation began in the magma body,

the non-volatile substances forming first with the result that the vapour-pressure of the more volatile substances was increased. Injection took place under a certain degree of directed pressure with the splitting off of the alkali-rich felspathic phase represented by the igneous parent (possibly trondhjemite) of the complexes, and finally by the late potash-pegmatites. This is the *Period of Injection Metamorphism*, and to it is most likely to be assigned the formation of the oligoclase-porphyroblast-schists; minor phases of post-consolidation date are indicated by the formation of myrmekite, shimmer-aggregates, etc.

On this interpretation, the various parts of G. BARROW's "Older Granite" represent late differentiates from an underlying magma which itself may be responsible for the high metamorphic condition of the country-rocks over the area in which its derivatives are now found. Both injection and high-grade metamorphism are results of the same cause, namely, deep burial in the mountain-region.

V. M. GOLDSCHMIDT [26, pp. 136-139] has assembled certain evidence which suggests that the igneous rocks closely associated with mountain-building are of granodioritic or trondhjemitic character. In Scotland, this generalisation seems to apply. The Cromar complexes, definitely associated with the epoch of movement, appear to have been formed by the injection of trondhjemitic material. Again, the great "granitic" complexes of the Lairg and Rogart districts of Sutherland [43, pp. 151-2; 44, pp. 20-40] are connected with the Lairg-Rogart granodiorite. Lastly, the Moor of Rannoch granodiorite [45, pp. 62-70] forms very fine complexes with the country-rock. Both these granodiorites show directed structures presumably produced by their intrusion during the last stages of the movements.

## V. THE YOUNGER GRANITES.

The last phase of igneous activity in the Cromar district to be considered here is that of the Younger Granites. This group of intrusions came into place after the movements had ceased. They may be considered for the purposes of this paper under three heads:—

1. Coull Granite.
2. Tomnaverie Granite.
3. Biotite-porphyrity Dykes.

### 1. *Coull Granite.*

To the east of Coull, the great ridge of Craiglich and Mortlich is formed of a coarse-grained pink granite which may conveniently be called the *Coull Granite*. The boundary between the injection-complex and the Coull Granite runs along the glen between Queen's Hill and Mortlich by the farm of Bonnyside. The actual contact is not well seen, but it can be stated that the granite truncates the structures of the Biotitic Complex. South of Bonnyside where in fig. 1 the granite projects into the Queen's Hill quartzite, a finer-grained rather felsitic margin to the granite is seen. Small apophyses of granite, brick-red in colour and felsitic in appearance, penetrate the quartzite here, but there is no development of injection-phenomena. South of Coull, poor exposures show the Coull Granite associated with hornblende-schists.

*Petrography.*—In hand-specimens the Coull Granite is a pink or reddish, coarse-grained rock showing blebs of milky quartz and very scanty mafic components. There is no appearance of fluxion, foliation, or any directed structures. In slice, microcline forms large shapeless plates enclosing euhedral small crystals of albite-oligoclase (approximating to  $Ab_{85}An_{15}$ ). Orthoclase is rare in subhedral grains. Quartz occurs between the feldspars. Scarce chloritised biotite completes the rock. An analysis of the Coull Granite is given in Table D.



TABLE D.  
*Younger Granites.*

	I.	II.
SiO <sub>2</sub>	70.30	67.96
Al <sub>2</sub> O <sub>3</sub>	12.67	15.06
Fe <sub>2</sub> O <sub>3</sub>	0.80	0.45
FeO	1.42	1.84
MgO	1.40	1.44
CaO	1.44	2.82
Na <sub>2</sub> O	4.70	4.33
K <sub>2</sub> O	3.88	3.04
H <sub>2</sub> O+	1.20	1.04
H <sub>2</sub> O—	0.50	0.50
CO <sub>2</sub>	nil	nil
TiO <sub>2</sub>	1.40	1.20
P <sub>2</sub> O <sub>5</sub>	0.09	0.14
S	nil	nil
MnO	trace	trace
ZnO	0.17	trace
Totals	99.97	99.82

I. *Coull Granite*, Summit of Mortlich, Aboyne, Aberdeenshire. *Anal.*, W. H. HERDSMAN.

II. *Tomnaverie Granite*, Tomnaverie Quarry, Tarland, Aberdeenshire. *Anal.*, W. H. HERDSMAN.

### 2. *Tomnaverie Granite.*

North and north-east of the Tillyhermack Hornblendic Complex a grey medium-grained biotite-granite is seen. It is extensively quarried at Tomnaverie near Mill of Wester Coull; it will be called the *Tomnaverie Granite*. The relations of the Tomnaverie Granite to either the Coull Granite or to the Cromar Complex are not seen. So far as exposed the Tomnaverie Granite is uniform, quite without directed structures and seemingly devoid of xenoliths. It is best considered to be a part of the Younger Granites.

*Petrography.*—The granite is grey in colour and shows a considerable amount of biotite. In slice, the components are seen to be quartz, microcline, acid oligoclase, orthoclase, and biotite; sphene, magnetite, and apatite are accessory. The potash-felspars form large shapeless plates and enclose the euhedral plagioclases. The oligoclase is zoned and always shows good crystal boundaries. The biotite is pleochroic from pale yellow to deep sepia, and is much more abundant than in the Coull Granite.

An analysis of the granite from Tomnaverie Quarry is given in Table D, above.

### 3. *Biotite-porphyrite Dykes.*

Half a dozen or so dykes of porphyrite have been noted cutting through the Biotitic and Hornblendic Complexes. For instance on Craig Dhu, several dykes and small bosses are seen; others occur on Scar Hill and further west towards Tillyhermack. These dykes are essentially alike; they are later than the complexes and are to be connected with the Younger Granite period of intrusion.

*Petrography.*—In thin slices, all these dykes are seen to be similar and composed of pheno-



crysts of plagioclase and biotite in a fine-grained base of plagioclase laths, biotite flakes, and interstitial quartz. The euhedral plagioclase phenocrysts are beautifully zoned and show variations from internal labradorite to external oligoclase-andesine. The biotite phenocrysts are well shaped and pleochroic from greenish-yellow to greenish-brown.

*Character of the Younger Granite Intrusions.*—The analyses of the two Younger granites are plotted, in relative molecular percentages of total alkalis, alumina, lime, and mafic oxides, in the diagram of fig. 7. With these is shown the average of 236 granites of all periods calculated by R. A. DALY (*Igneous Rocks and Their Origin*, 1914, p. 19). The various slight differences between the Cromar Younger Granites and DALY's average can be readily seen from

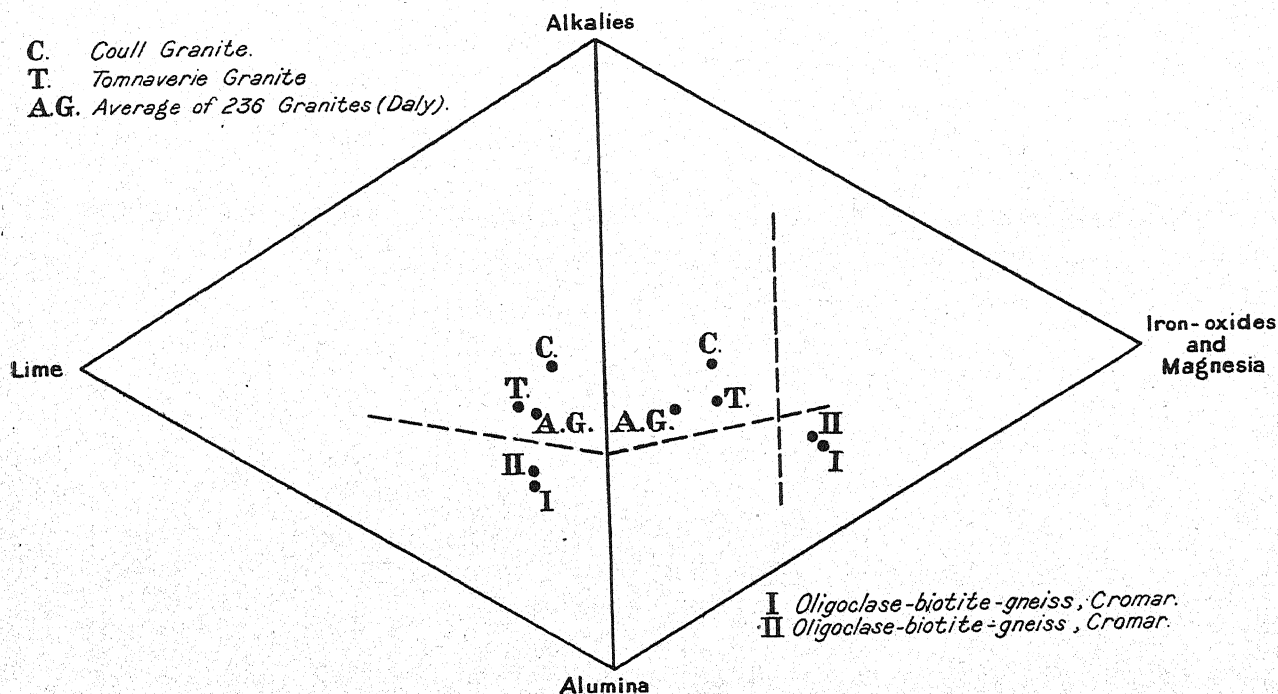


FIG. 7.—Comparison of the Oligoclase-biotite-gneiss and the Younger Granites of Cromar.

the figure. When a comparison is made with the analyses of the oligoclase-biotite-gneiss given on p. 329, fundamental differences are revealed, as shown in the figure. The much greater content of alumina and of mafic oxides in the gneiss causes a wide separation in the position of the two groups of analyses. It may be found possible as research progresses amongst the acid igneous rocks of North-east Scotland to lay down some such chemical criteria for their distinction as are suggested above.

The biotite-porphyrites are connected with the Younger Granite intrusions on the evidence of their geological habit and their petrographic characters.

The Coull and Tomnaverie Granites belong to the great group of granites of North-east Scotland styled Younger or Newer Granites by the Geological Survey. The members of this group agree in being of later date than the movement period, but it is probable that individual granites may be of somewhat different ages.

It may be said, at all events, that the Coull and Tomnaverie Granites were intruded after the mountain-building movements had ceased; the country-rock was relatively cold at the time of intrusion as shown by the occurrence of chilled marginal facies. Intrusion was not under directed pressure; there were no injection-phenomena and the pegmatite phase was

not separated from the magma. On the other hand, intrusion outside the main body takes the form of porphyrite dykes along tension fissures.

## VI. SUMMARY OF THE IGNEOUS HISTORY OF CROMAR.

From what has been said before, the igneous history of the Cromar district may be summarised as follows:—

1. *The Geosynclinal Phase.*—During the formation of the geosyncline, igneous activity manifested itself as sills of doleritic or gabbroic character—the *Greenstone Series*. The keynote of the phase is gentle subsidence.

2. *The Movement Phase.*—Mountain-building movements in the geosyncline resulted in the production of the *General Metamorphism*. In Cromar the impression of the metamorphic character on the sedimentary country-rocks and the Greenstone Series is believed to have been accompanied by the intrusion of a large body of possibly *granodioritic magma*. To this combination of factors is due the high metamorphic grade of the Deeside rocks. After the culmination of the crustal movements, solidification began in the underlying magma with the resultant splitting-off of a soda-dominant *trondhjemitic fraction*. This fraction, injected under some pressure into the already metamorphosed country-rocks, is the igneous parent of the *Biotitic and Hornblendic Complexes*; the major rocks of these complexes are mixtures of various kinds between the igneous and country-rock components. To this period is assigned the *Injection-metamorphism* shown, it is considered likely, by the passage of soda-rich solutions into the country-rock with the production of oligoclase-porphyroblast-schists. The keynotes of the Movement Phase are, (1) the country-rocks were at a high temperature; (2) the region was under strong stress; (3) intrusions are concordant.

3. *The Post-movement Phase.*—After the total cessation of the crustal movements there occurred the intrusion of the *Younger Granites*—the microcline-oligoclase-granites and biotite-porphyrites. The keynotes of this phase are, (1) the country-rocks were cold at the time of intrusion; (2) they were under no stress; (3) the intrusions are discordant.

In conclusion, the question of the possible connection between the three phases may be briefly touched upon. General opinion among Scottish geologists appears to favour a close connection between the Greenstone Series and the Older Granites of the Movement Phase; parts of the Older Granite consolidated before the maximum crustal movements. On the other hand, the Older and Younger Granites have always been kept completely separated. G. BARROW [9, p. 282] holds that the Older Granite is of pre-Torridonian age. The Younger Granites have been taken to be of Devonian date and have been connected with the Caledonian movement (*cf.* A. HARKER [28, p. lxxxi, *et seq.*]). With the question of the age of the Older Granite is intimately connected that of the metamorphism. Concerning the date of the metamorphism, two views are more or less current, the one holding that the date is pre-Torridonian, the other Caledonian or Lower Palæozoic. In the absence of unequivocal evidence, this question must be left open. Cromar supplies nothing new with regard to it.

It must be pointed out, however, that in the South Norwegian portion of the Caledonian chain, V. M. GOLDSCHMIDT [24, 26] has described two families of rocks, both believed to be of Lower Palæozoic age, which bear the closest resemblances to rocks of two of the Cromar phases. GOLDSCHMIDT's Green Rocks contain many types that can be matched in the Greenstone Series of Scotland, whilst his injection-rocks connected with trondhjemite are exactly reproduced by rocks of the Cromar Complexes. This general similarity does not necessarily imply similarity of age, but may express similarity in type of crustal movement.



It may well be that igneous activity in Cromar gives a connected record of events during a single movement-period, namely, first the intrusion of basic sills, next the injection of concordant trondhjemitic material, and finally the intrusion of discordant granites. Comparative studies may yield evidence on this question.

Finally, the writer desires to pay a sincere tribute to Mr GEORGE BARROW, who blazed many a geological trail amongst the complexities of Highland Geology. The paths opened up by Mr BARROW have been departed from to a small extent—departures due to detailed study of a small area. The main lines of Mr BARROW's work, however, will remain secure as a monument to his pioneer genius.

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XV.—On the Feeding Mechanism of *Nebalia Bipes*. By H. Graham Cannon, M.A., D.Sc., F.L.S., Professor of Zoology in the University of Sheffield. (With Seven Text-figures.)

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INTRODUCTION.

The object of this research was to compare the feeding mechanism of *Nebalia* with that of *Hemimysis* described by Miss MANTON and myself (1927). The observations of the living animals were made partly at Naples while I was occupying the Cambridge University table, and partly at Plymouth where I had the use of the London University table.

The methods used in determining the feeding currents were the same as those used for *Hemimysis* (CANNON and MANTON, 1927). To obtain a ventral view of the trunk limbs, I simply held the living animal upside down, gripping the abdomen with a pair of forceps, and in this position it would feed for a long time. I found it possible even to remove the entire carapace without killing the animal or upsetting the normal movements of the limbs.

To study the arrangements of the trunk limbs and mouth-parts ordinary methods of dissection were useless as these disarranged the extremely fine setal armature. To overcome this, I embedded the animals in paraffin wax and then cut the block on a microtome down to any desired level, *e.g.* the sagittal plane. Then I unmounted the block and dissolved away the wax with xylol. The remaining portion of the specimen was then placed in absolute alcohol, then glycerine, and finally mounted in glycerine jelly. In this way I have obtained mounted material showing all the necessary aspects of a limb, and I can be certain that the setæ on that limb are in a perfectly normal position.

HABITS.

The habits of *Nebalia* were described by SARS (1896, pp. 30–32), but he did not deal in any detail with the feeding mechanism.

*Nebalia* is a mud-living form found commonly round our coasts, usually under stones. CALMAN (1909, p. 159) states that *Nebalia bipes*, the form found both at Naples and Plymouth, is very resistant to unfavourable conditions, "thriving in water which is foul with decaying matter." I thus found it very easy to keep specimens under observation in the laboratory. When placed in a dish of sea-water with a layer of mud at the bottom, *Nebalia* makes straight for the mud and buries itself just below the surface. It remains still, with only the trunk limbs moving, sometimes for a considerable period; but often even the trunk limbs are still, so that the animal is perfectly motionless. In this condition the pulse of the heart becomes very slow, but quickens directly the trunk limbs begin to move again.



SARS (1896, p. 31) states correctly that the trunk limbs take no part in locomotion, but he continues, "By the play of these appendages there is produced, namely, inside the valves of the carapace, a forward current of the water by which the small particles that serve the animal for food are drawn into the area of the oral parts. The water during this flows out in a continuous stream from the foremost extremity of the carapace below the frontal plate." This statement has been copied by CALMAN (1909, p. 159), but it is incorrect. A current of water enters the carapace anteriorly. It is sucked in by the trunk limbs and passed out postero-ventrally. The current is filtered by an elaborate arrangement of setæ arranged on the inner edges of the trunk-limb endopodites, and the food so gathered is passed forward to the mouth-parts.

#### ARRANGEMENT AND MOVEMENT OF TRUNK LIMBS AND MOUTH-PARTS.

The carapace completely covers the trunk limbs, the mouth-parts with the exception of the tip of the mandibular palp, and the basal part of the antennæ. The long setose flagella of the antennæ curve backwards and run parallel with the recurved distal parts of the trunk-limb endopodites, which close the median space between the ventral edges of the carapace. In this way there occurs a tubular space between the trunk limbs that I call the "filter chamber." It is closed in dorsally by the ventral body-wall, laterally by the proximal parts of the trunk-limb endopodites, and ventrally by the mat of long setæ borne on the recurved tips of the trunk limbs. It is open anteriorly and the entrance is guarded by the antennules, the eyes, and the rostrum. By bringing the antennules down parallel to the antennæ, slightly depressing the eyes, and bringing the rostrum down to cover the space between the antennules this entrance can be completely closed.

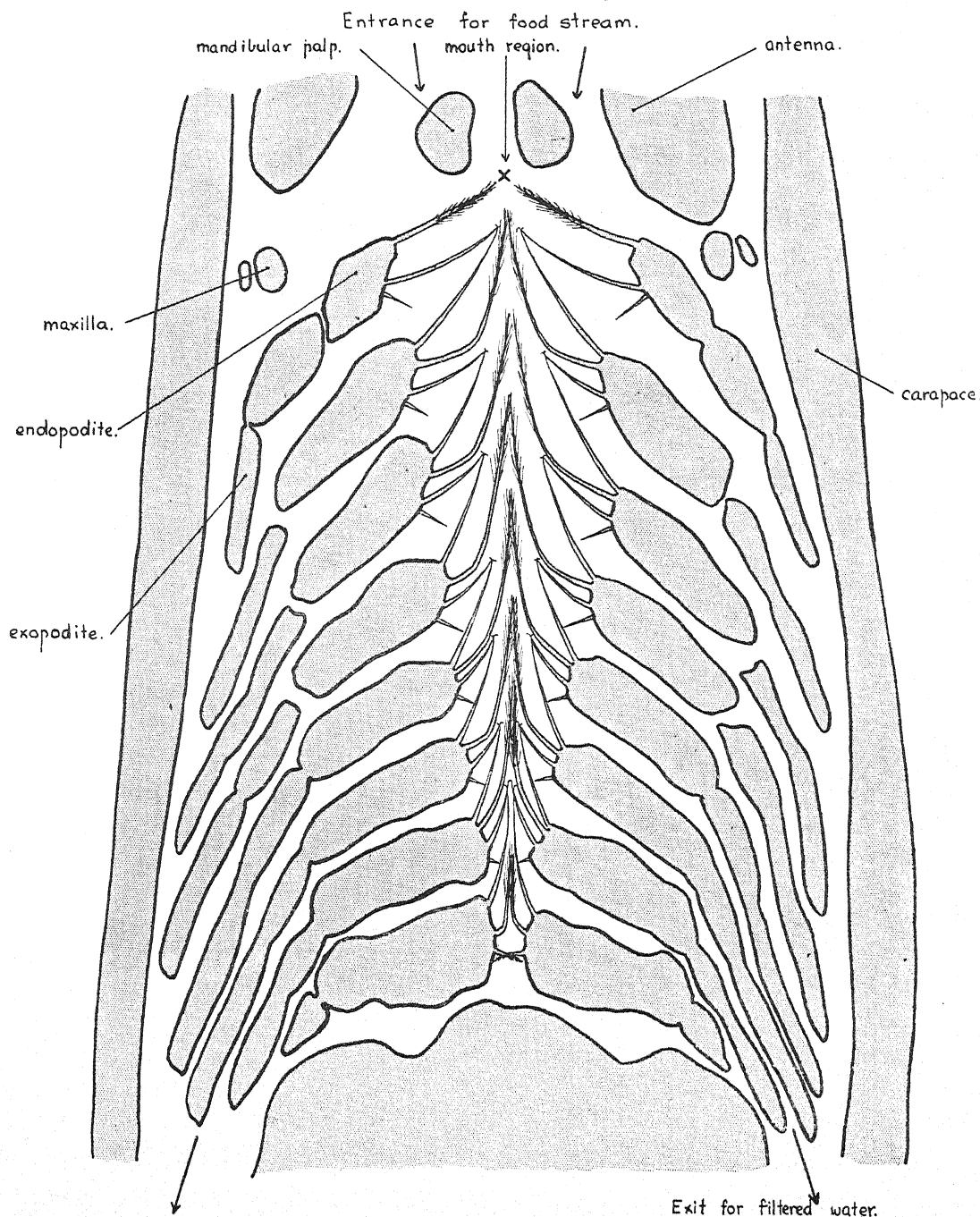
The rostrum appears to control the current entering the filter chamber. By partially depressing it the entering food-stream is divided into two, the upper portion passing dorsally over the rostrum, the lower entering the filter chamber. This movement is brought about, as CLAUS (1889, p. 39) observes, not by special rostral muscles, but by muscles controlling the front part of the head, the eyes, and the antennules.

Normally the rostrum is elevated and the antennules project laterally. Periodically they are swept backwards in an oar-like motion and the pleopods are jerked backwards. These movements push the animal forwards through the mud, but also sucks in mud towards the entrance to the filter chamber. The lateral movement of the antennules must produce a region of low pressure just below the rostrum, and so mud particles pass towards this region and these are then sucked in by the trunk limbs.

The trunk limbs project at right angles to the ventral body-wall, their setose tips passing back at a right angle to the main axis of the limb. As the limbs diminish in length from before backwards, these distal parts overlies each other, forming a thick mat of setæ, and this is the floor of the filter chamber. The planes of the flattened endopodites of the first pair project backwards at about  $40^\circ$  to the median plane, and this angle increases in passing backwards to the eighth pair, which project almost at right angles (text-fig. 1). The exopodites and epipodites of all these limbs project backwards and overlies each other like the leaves of a book. The inner edges of the endopodites are much further apart anteriorly than in the posterior limbs. The eighth pair, as will be described in more detail later (p. 362), are linked together by two rows of feathered setæ so as to form a continuous plate.

In order to determine the mechanism by which the trunk limbs produce the food-current the movement of each limb was followed separately. This was made possible owing to the

fact that the limbs are often stationary, and when they recommence to move rhythmically they do not all commence at the same time, and it is easy to determine the order and mode of



TEXT-FIG. 1.—Diagram based on a frontal section and a frontal slice, to show the arrangement of setae on the trunk-limb endopodites and the passage of the food stream.

movement of each limb. When this had been done the results were plotted diagrammatically (text-fig. 2), and from this the current-producing mechanism can be deduced.

The main features of the trunk-limb movements which can be observed directly are as follows:—

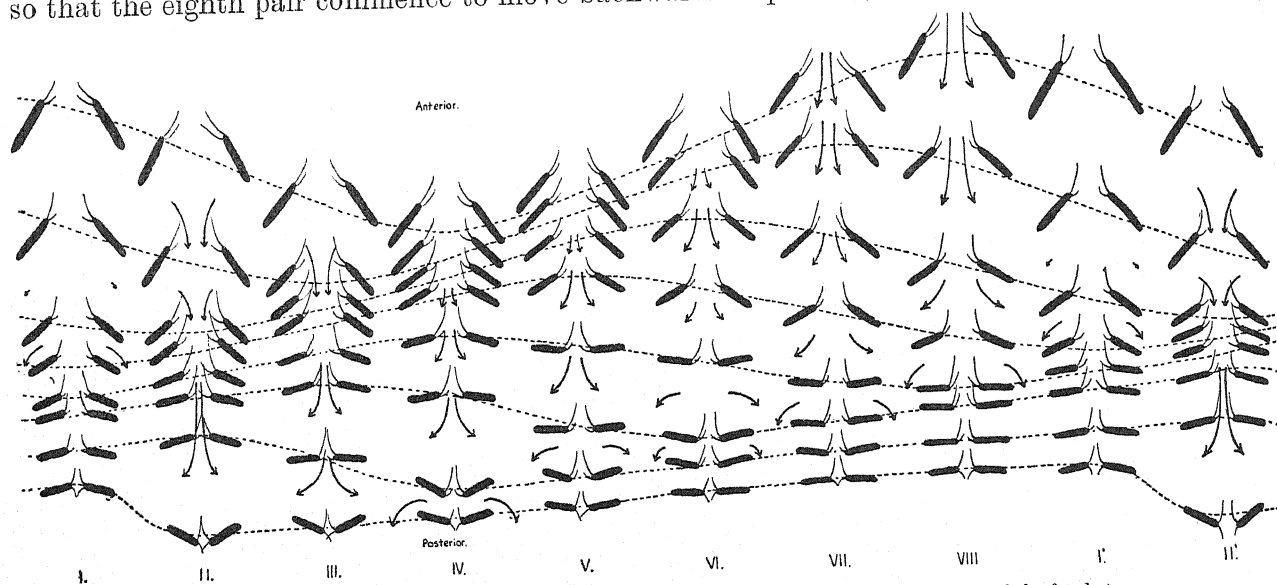
1. The limbs move backwards and forwards rhythmically.
2. The posterior limbs move backwards before the anterior.

3. The amplitude of the first pair is the greatest. This diminishes back to the fifth pair. The amplitude of the fifth to eighth pairs is approximately the same.

4. The first four pairs of limbs move backwards and forwards in a normal periodic manner, while the last four move backwards more quickly than they move forwards, this being most pronounced in the eighth pair and diminishing forwards to the fifth pair.

5. The last four pairs of limbs, in moving backwards, rotate about their axes, so that the inner edge of the endopodite passes further back than the outer edge. This again is most pronounced in the eighth pair and diminishes forwards.

In text-fig. 2 these observations have been recorded graphically. The movement of the limbs has been divided into eight phases of which the first represents the limbs approximately in their position at rest. By following the dotted lines from left to right the movement of any pair of limbs can be followed through a complete oscillation. The diagram has been drawn so that the eighth pair commence to move backwards in phase I, the seventh in phase II, the



TEXT-FIG. 2.—Diagram to show the oscillatory movements of the trunk limbs and the passage of the food stream.

sixth in phase III, and so on. Between phase I and II the eighth pair move backwards to their fullest extent, rotating inwards at the same time. They take from phase II to phase I' to return to their normal position. The seventh pair take from phase II to phase IV to move backwards, and from IV to II' to return again. They do not rotate backwards so much as the eighth pair. The sixth take from III to VI to move backwards, and the fifth from IV to VIII and so on. The fourth pair show normal periodic motion, and from the fourth to the first pair the amplitude increases and the back-stroke becomes progressively later.

The water currents can be deduced from this chart. Firstly, water cannot pass into the filter chamber from behind, because the eighth pair of limbs are interlocked by a mat of feathered setæ (p. 362). It cannot pass in laterally, because the exopodites and epipodites overlies each other in such a way that water in attempting to pass in from outside would simply press them closer together. These structures are thin and not very rigid, and their valvular action can be understood by comparing them with the leaves of a book, their attachment to the main axis of the limb corresponding to the binding of the book. Water could be forced between the pages from the binding outwards, but not in the reverse direction, or, more strictly, in the latter case either the pages would stick together or a large space would be established between two consecutive pages, but nothing corresponding to this takes place



in *Nebalia*. There is no marked and persistent gap between any two epipodites. The water is prevented from entering the filter chamber ventrally by the mat formed by the distal ends of the trunk-limb endopodites. Anteriorly the filter chamber is, during normal feeding, open, and it is from this direction that water enters.

Between phase I and II the space between limbs 7 and 8 is increased by the backward and rotational movement of the eighth limbs. There is not much room for the limbs to move backwards owing to the ventrally projecting first pair of pleopods, but this decreased amplitude is counterbalanced by the inward rotation of the limbs. This must suck water from the anterior part of the filter chamber backwards. Between phase II and III water is similarly sucked backwards into the space between trunk limbs 6 and 7 by the backward motion of the seventh pair. But, at the same time, the space between the seventh and eighth limbs is diminished, and this forces water out from the posterior part of the filter chamber between the exopodites and epipodites of the seventh and eighth limbs to the exterior. The suction of water by the other limbs can be similarly followed. It will be readily seen that wherever, in passing from one phase to the next, the distance between any adjacent pair of dotted lines increases, this indicates that the space between the limbs represented by those dotted lines is increasing, and therefore water must be sucked into that space. Thus, from phase V to VIII it can be seen that water is being sucked in *from the outside* into the anterior part of the filter chamber. This water does not pass out between the exopodites of the anterior limbs as it does posteriorly, because, before it has time to do this, the eighth pair of limbs suddenly jerks back (between phase I and II) and so draws this water back to the posterior part of the chamber before passing it to the exterior. In this way all the water entering anteriorly is forced to pass practically the whole length of the filter chamber.

Thus, while all the endopodites can be termed inhalent pumps, only the posterior ones act as exhalent pumps, and that they are real pumps and not mere valves can be seen from the diagram. As the space between the seventh and eighth limbs is diminished, the inner edges of the endopodites come closer together than the outer, so that water must be forced out laterally. The exopodites and epipodites are the only parts of the limbs acting as true valves.

The above description applies to the normal quick-feeding movement. When the animal becomes sluggish there is no noticeable difference between the movement of the anterior and posterior limbs.

#### THE FILTER MECHANISM.

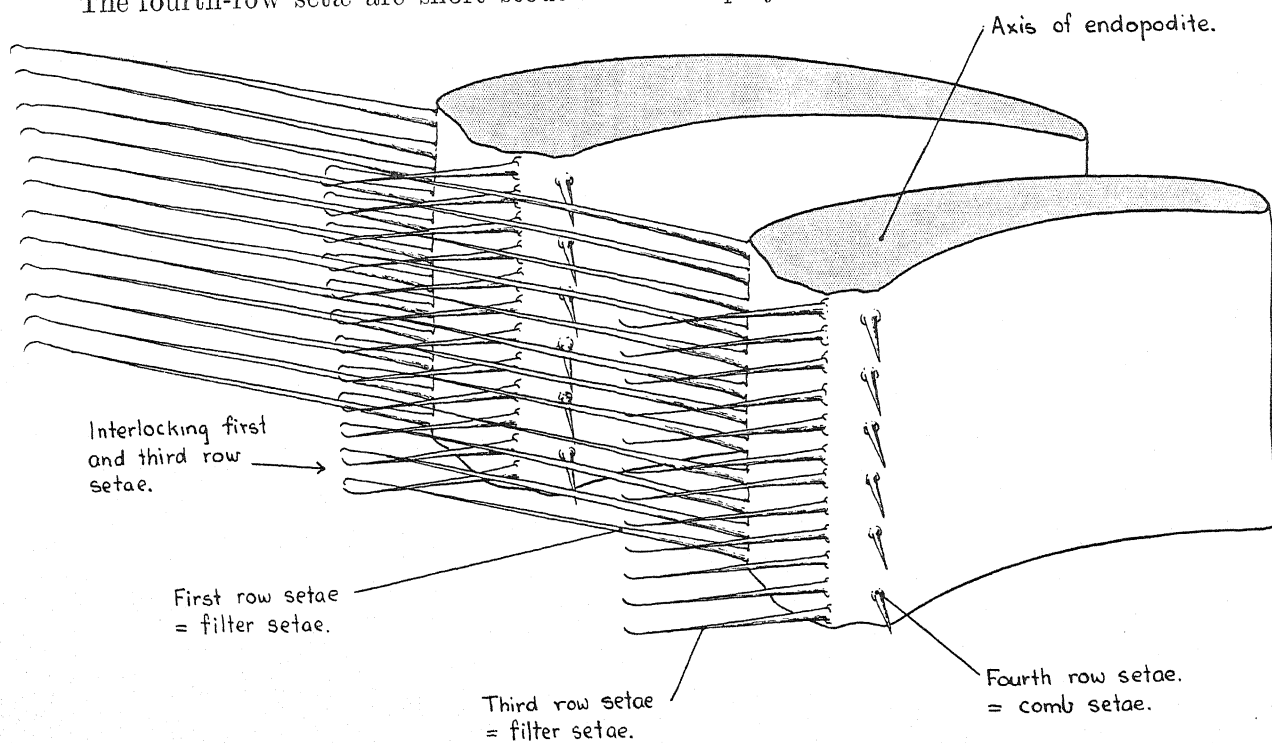
In order to describe how the trunk limbs filter off the food particles, the setæ arming the inner edges of the trunk limbs must first be described. The setæ of the first and eighth limbs differ from the remainder, and so one of the middle limbs will be described.

There are four rows of setæ projecting from the inner edge of the endopodite (text-fig. 1). The first three project antero-medially, while the fourth projects postero-medially. The first and third rows form the actual filtering walls of the filter chamber. They consist of extremely fine, closely set setæ irregularly feathered with minute setules, too fine to represent without exaggeration in any of the figures. The anterior tips of the first-row setæ project in between the third-row setæ of the limb in front. In addition, the tips of the setæ are hooked. Those of the first row curve inwards and downwards, those of the third row curving inwards and upwards (text-fig. 3). In this way the setæ of the first and third rows are hooked together in a manner reminiscent of the barbules and barbicels of a feather. They thus form one continuous zigzag wall on either side of the filter chamber (text-fig. 1). Although it cannot be observed directly it is extremely probable that in the oscillations of these limbs

this filter wall is never broken. The setæ can slide over each other, but their hooked ends and their elasticity prevents any gap occurring between the limbs.

The first row extends from the base of the limb up to the setose tip. The third row extends from about the middle of the coxopodite up to the second joint of the endopodite. The hooked endings become less pronounced towards the distal end of the limb, but also the setæ of the first row that have no corresponding third-row setæ, namely, those occurring on the basal part of the coxopodite, have no hooks at all. They are simply forwardly directed straight setæ, more robust than the remainder of the row, and can be looked upon as groups of gnathobasic setæ (text-fig. 4a).

The fourth-row setæ are short stout setæ that project backwards in between the first-



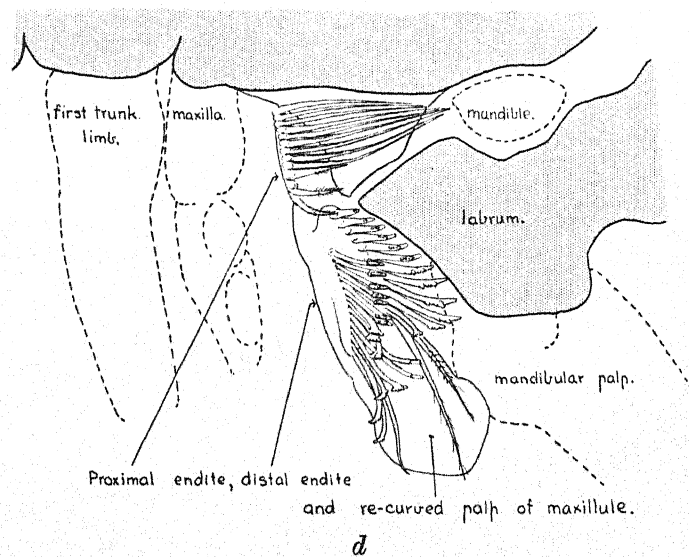
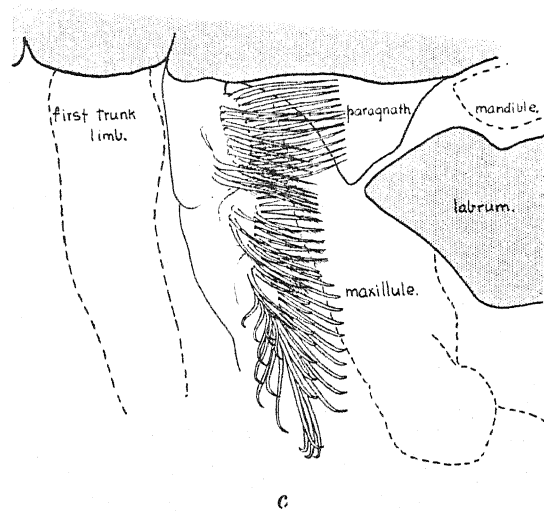
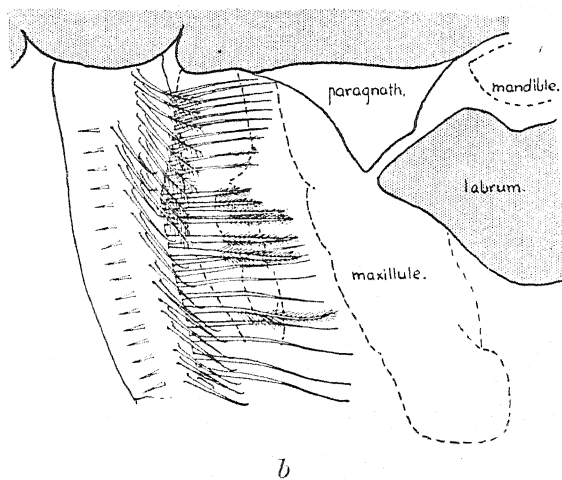
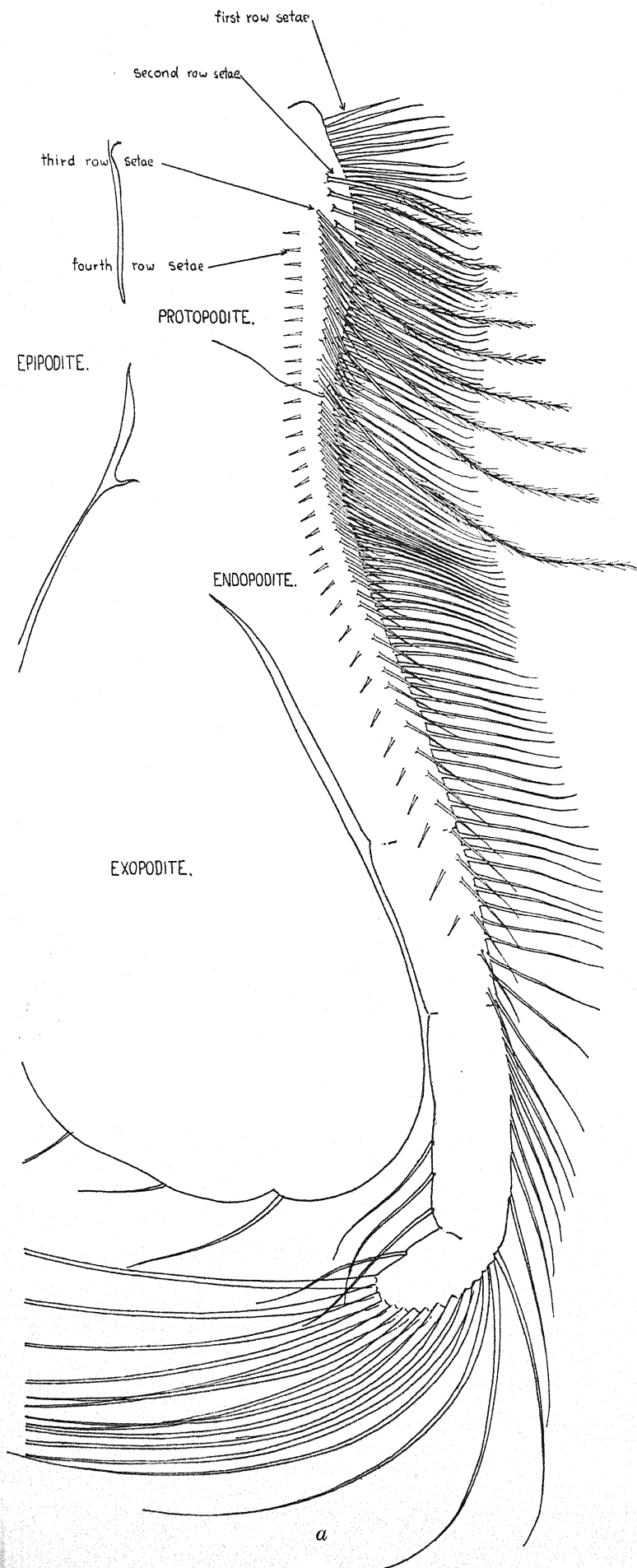
TEXT-FIG. 3.—Stereogram of portions of two trunk-limb endopodites (distal to brush setæ) viewed obliquely from above to show the constitution of the filter wall and the position of the comb setæ.

row setæ of the limb behind (text-fig. 3). They extend the whole length of the third row, but are not as numerous (text-fig. 4a).

The second row consists of ten long, heavily feathered setæ situated on the distal two-thirds of the coxopodite. The proximal seta is about the length of one of the first-row setæ, but the length increases until the distal seta is just over twice this length. They pass ventro-medially and then turn sharply forwards (text-fig. 4a).

CLAUS also describes this setal armature (1889, pp. 28-29). The first row he calls the "randständige Reihe, RR," the second the "Zwischenborsten, ZB," the third the "Seitenreihe, SR," and the fourth the "Nebenreihe, NR." Unfortunately, in his fig. 2, Taf. 4, which has become the classical figure of the *Nebalia* trunk limb, the row RR is wrongly labelled, and in fig. 5, Taf. 4, either the setal rows are incorrectly labelled or else the epipodite and exopodite are figured on the wrong side of the limb. CLAUS does not mention the interlocking of the first and third rows.

Food particles entering the food chamber are mostly caught on the long-feathered, second-row setæ and then passed forwards to the mouth-parts. This much can be observed

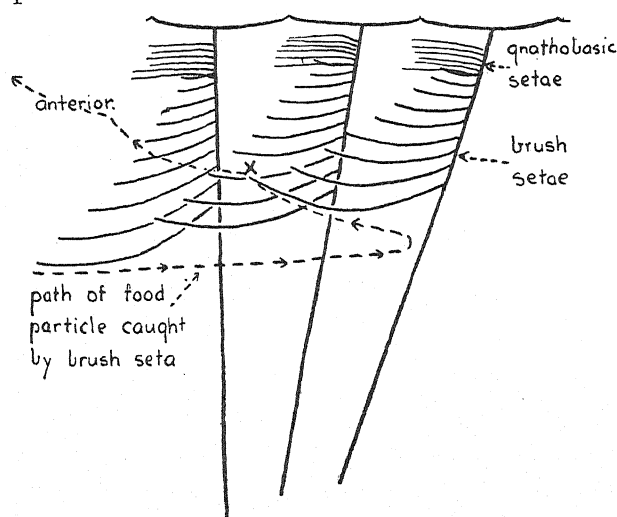


TEXT-FIG. 4.—Sagittal views of parts of the maxillules, maxillæ, first and second trunk limbs. All these figures were drawn from a microtome-cut sagittal slice.  
*a*, Second trunk limb; *b*, First trunk-limb protopodite; *c*, Proximal part of maxilla; *d*, Proximal part of maxillule.



under the microscope. Any particles that happen to get past these "brush setæ" will pass with the current on to the filter walls formed by the first- and third-row setæ, and here they will be deposited. They will then be combed off by the stiff setæ of the fourth row and pushed back into the filter chamber. Here they will either be caught by the more posterior brush setæ or they will pass back with the food stream and be filtered off by the more posterior parts of the filter wall. They will then be again combed off, but ultimately, as the filter chamber becomes narrower, they must be caught on the brush setæ.

In the backward and forward movement of the limbs the brush setæ must swing periodically up towards the food groove. Owing to this and to the fact that the distal brushes are much longer than the proximal, and further, that the phase of the posterior limbs is always in front of the more anterior, food gathered on any brush seta will be passed forwards and upwards towards the mid-ventral line. Thus in text-fig. 5 a particle on the distal brush seta



TEXT-FIG. 5.—Diagram to illustrate the action of the brush setæ in sweeping food particles upwards on to the gnathobasic setæ. The axes of three trunk limbs are indicated by the three long thick lines.

of the posterior limb will, in the most anterior position of the limb, reach the spot X on a level with the seventh seta of the limb in front. In its backward movement, which will take place before that of the limb in front, the brush setæ of the latter, since they are heavily feathered and point forwards, will brush the particle off the seta of the posterior limb so that the particle will become shifted both forwards and upwards towards the gnathobasic setæ on the proximal parts of the limbs.

Thus, to summarise the filtering action of the trunk limbs, suspended food is gathered chiefly on the second-row brush setæ of the anterior limbs. Any stray particle is filtered off by the first- and third-

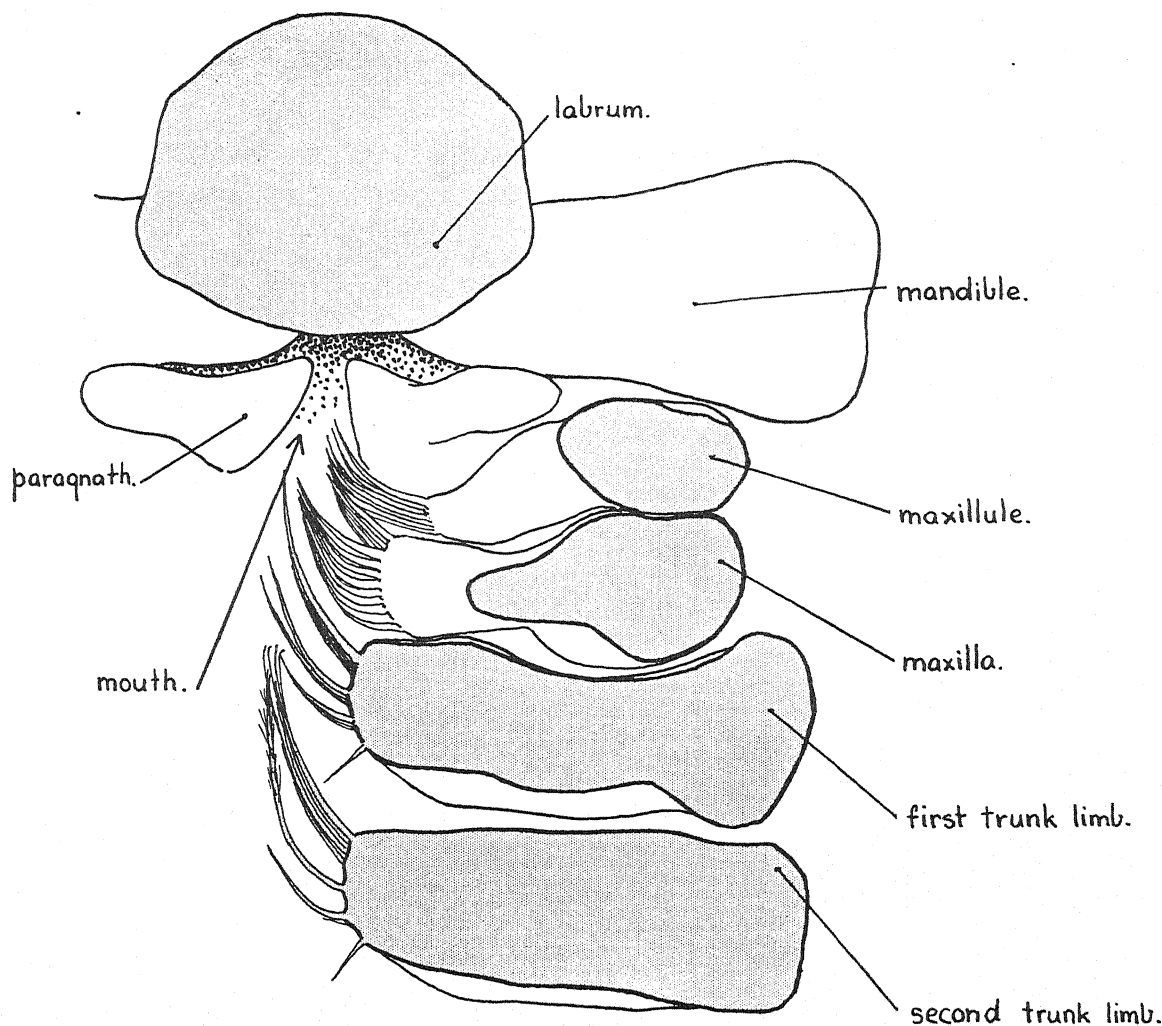
row filter setæ, combed off again by the fourth-row comb setæ, and ultimately caught by the more posterior brush setæ. The brush setæ automatically pass the food upwards towards the mid-ventral food groove. Here the only setæ forming the walls are the stiff proximal gnathobasic setæ of the first row, and they simply pass the collected food forwards on to the mouth-parts.

It has already been mentioned that the first and eighth trunk limbs differ in their setal armature from the others. On the eighth limb the first row is normal, but the second row is represented by about six or fewer brush setæ. The fourth row is absent, as might be expected from the function of this row in more anterior limbs. The third row project medially and slightly backwards, and interlock with their neighbours from the other side. They are covered with setules and so form a mat that effectively prevents particles entering the filter chamber from behind.

On the first trunk limb the third and fourth rows are normal. The second row consists as in the normal limb of ten setæ, but these are all arranged close together on the proximal half of the coxopodite. They are heavily brushed, but are shorter than the normal. The first-row setæ are not hooked, and again this might have been expected. An additional difference in this row is that setæ 11 to 16 and seta 21 are very stout and heavily armed with setules. This arrangement is constant in all the specimens examined. From text-figs. 4b and 4c it

can be seen that the group of setæ 11-16 overlies the second endite of the maxilla, while seta 21 stretches across the third endite. CLAUS, in his figure of this limb (1889, Taf. 3, fig. 10), does not indicate these differences. The first row of setæ have not developed the filtering function. They function in pushing the food forwards on to the mouth-parts so that these first trunk limbs might be termed maxillipeds.

The collected food mass is manipulated into the mouth by the true mouth-parts. These



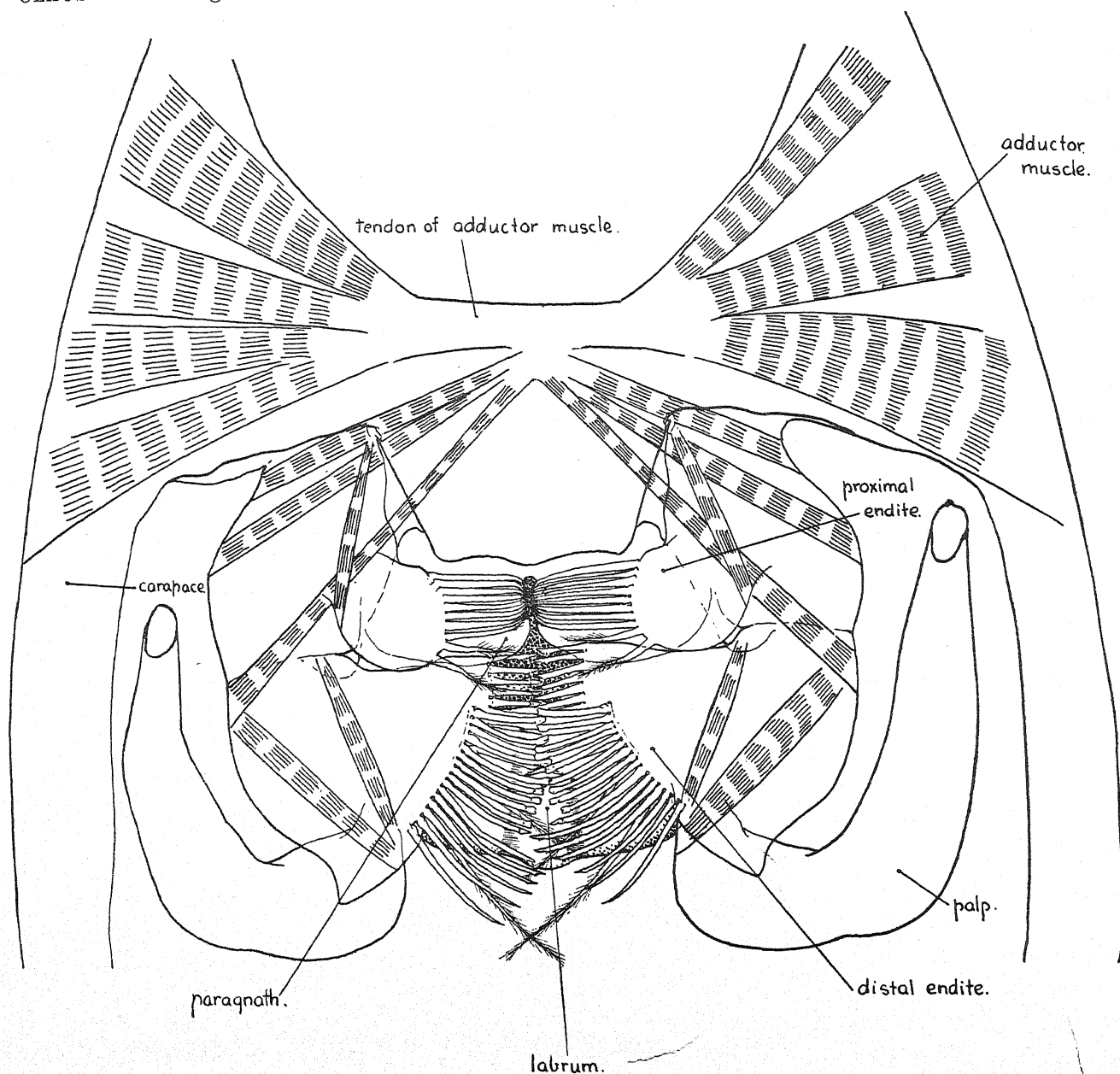
TEXT-FIG. 6.—Drawing of an oblique frontal slice to show the arrangement of the mouth-parts.

have been described in detail and figured by CLAUS (1889), but in certain essential points his descriptions are lacking and his figures incorrect.

The upper lip is similar to that of *Mysis*, but as the incisor processes of the mandibles are very small and widely separated, and thus do not act as biting parts, the labrum extends backwards underneath the molar processes more than in a *Mysid*. The entrance to the mouth from the tip of the labrum thus slopes forwards and upwards instead of directly upwards. The lower lip is deeply cleft as in all primitive Malacostracan groups.

The maxillule bears two endites and a long recurved palp similar to that of the primitive *Mysid* *Gnathophausia*. The distal endite bears two rows of large spatulate setæ and a few feathered ones (text-fig. 4d). The proximal endite bears nine long, thin setæ covered with minute setules on their posterior (median) surface, and distally three short, stout, feathered

setæ. The distal endites are biting parts, and bite together in a transverse plane. The setæ of the proximal endite curve forwards close against the inner face of the paragnaths (text-figs. 4*d* and 6), so that the planes of the setæ of the two endites are practically at right angles. CLAUS did not figure this for *Nebalia*, but in a very rough sketch (1889, Taf. 3, fig. 9) he



TEXT-FIG. 7.—Drawing of a transverse slice to show the musculature of the maxillule and its relation to the mouth.

figured it for *Paranebalia*, but unfortunately it is the *Nebalia* figure that has found its way into text-books.

The lateral biting movement of the distal endites is brought about by a series of powerful muscles attached to the endoskeleton of the adductor muscle (text-fig. 7). This movement results in a forward movement of the proximal endites, and from the musculature (text-fig. 7) it is obvious that this forward movement is a passive one. The only musculature of the proximal endite is a small levator muscle.



The protopodite of the maxilla bears three endites. The second and third, arising from the basipodite, bear setæ which point inwards and slightly forwards and are arranged irregularly in three rows (text-fig. 4c). The coxopodite bears three rows which show a marked similarity to the first three rows of a middle trunk limb. The third row consists of three or four setæ only on the distal part of the joint. The second consists of ten setæ closely arranged as in the first trunk limb and projecting antero-medially. The first three of these setæ are longer and are not feathered as are the others. The first row consists of twelve fine setæ passing directly forwards to lie just inside the setæ of the proximal maxillary endite (text-fig. 6). Thus both in the maxillules and maxillæ the planes of the distal and proximal endites are at right angles to each other. CLAUS did not figure this, but it is obvious that this arrangement is of extreme importance in the feeding mechanism.

Food gathered by the more posterior trunk limbs will be only the minutest particles, and these, as explained above, will be passed into the ventral food groove and forwards by the gnathobasic setæ of the first trunk limb. From the first trunk limb they are passed forwards on to the basal endites on the maxilla, and thence on to the basal maxillary endite, and so direct between the paragnaths on to the molar processes of the mandibles.

Larger food particles cannot possibly get past the barrage of feathered setæ that they meet at the entrance to the filter chamber. Being large, they require mastication, and this is carried out by the distal maxillary endites. They are caught on the anterior food brushes and passed forwards between the maxillæ directly on to these endites. The maxillæ are usually held comparatively wide apart, and when the animal is feeding on a heavily laden food current, food accumulates in the space between them. It is then passed forwards by an intermittent, not rhythmical, inward motion of the maxillæ. The oblique arrangement of the setæ on the distal endites converts this motion partly into a forward one, and so the food is transferred on to the biting endites of the maxillules. A group of long setæ at the base of the maxillary endopodite also assist in this transfer. When food accumulates to any greater extent the mandibular palps are bent back and the food mass pressed directly towards the mouth. This has the double result of placing the food on the masticatory endites and at the same time blocks the way for any large food particle, and so holds up food gathering until the mass already gathered has been dealt with.

The masticating movements of the distal maxillary endites are upwards as well as inwards, as can be seen from the musculature (text-fig. 7), so that when the food has been masticated it is passed upwards on to the proximal endites and so on to the mandibles.

#### DISCUSSION.

The interest of the feeding mechanism of *Nebalia* is that it can be divided into two parts, firstly, one for feeding on large particles, and secondly, a true filter-feeding mechanism for minute particles. The interest of the former lies in its close similarity to that of *Hemimysis*; that of the latter, in that it is unique.

The chief difference between the mechanisms of feeding on large food of *Nebalia* and *Hemimysis* is that the former cannot readily pick up directly large food particles. The possession of a large carapace in correlation with mud-living habits in *Nebalia* makes this difficult, but not impossible, as I shall emphasise later on. Another difference is that *Nebalia* does not carry biting incisor processes on its mandibles, so that the preliminary mastication of food is carried out entirely by the maxillules and not shared with the mandibles as in *Hemimysis*. Correlated with this same difference is the absence of asymmetry between the

mandibles of *Nebalia*. In *Hemimysis* the marked asymmetry is of functional importance in transferring the food bitten by the incisor processes upwards on to the molar processes (CANNON and MANTON, 1927, p. 235).

Apart from these differences the similarity is very striking. The labrum, paragnaths, maxillules, and mandibular palps are very similar in the two forms, and, what is more important, the way in which the maxillules and mandibular palps function is the same. The structural similarities between the mouth-parts of *Nebalia* and Mysids have been dealt with in detail by CLAUS (1889, pp. 21-26). In addition, the first trunk limb in *Nebalia* differs from the more posterior limbs in being modified for pushing food towards the mouth, and this is exactly paralleled in *Hemimysis*. Both bear strong gnathobasic setæ on the protopodite.

The filter-feeding mechanism of *Nebalia* is a true filter, that is, a food-bearing current is passed through a definite sieve on which the filtered particles are deposited. In *Diaptomus*, according to STORCH and PFISTERER (1925), and in *Hemimysis* (CANNON and MANTON, 1927), a similar true filtering mechanism is to be found. But in *Nebalia* the filters are also the current producers. In *Diaptomus* the maxilla is a passive filter, the maxillule sucking water through it. In *Hemimysis* the filtering endite of the maxilla is also passive, but the vibration of the exite and, in fact, of the main part of the limb assists in sucking water through the filtering setæ. The main food current is, however, produced by the thoracic-limb exopodites, while in *Nebalia* the trunk-limb endopodites are alone responsible for both the production and the filtering of the food stream.

The filtering mechanism of *Nebalia* is unique among the Crustacea, whose feeding habits have hitherto been investigated. STORCH (1925, p. 83), in his attempt to derive all filter mechanisms from that of the modern Anostraca, finds similarities between *Nebalia* and such forms as *Chirocephalus*. He states that the eight trunk limbs of *Nebalia*, "even in their finer details," closely resemble the Phyllopodium, and quotes CLAUS (1889) in support. CLAUS certainly mentions the similarity between the two types of limbs, but proceeds at once (p. 26) to point out that a study of the limbs of *Paranebalia* establishes that the similarity is superficial and that the leaf-like limb of *Nebalia* evolved from a biramous "Schizopod" limb. But STORCH states further (p. 83), "Nach allem zu urteilen, was man über Bau und Lagerung diese Beine weisz, sowie insbesondere auch über den Bau der Mandibel und der beiden Maxillen, stehe ich nicht an, die Vermutung auszusprechen, dasz auch von den Mundgliedmaszen und Thorakalbeinen der Leptostraca ein ganz ähnlicher homopodialer Fangapparat mit ganz ähnlichen, zum Teil von den homologen Beinabschnitten zusammengesetzten, zum Teil (Vorbringevorrichtung) freilich in anderer Weise gebildeten Teilmechanismen zusammengesetzt wird, wie wir ähnlich bei den homopodialen Phyllopoden (insbesondere den Anostraca und Ctenopoda) kennen gelernt haben." In this quotation he does not state definitely that there are structural similarities between the trunk limbs and mouth-parts of the two forms, but it is a mere valueless conjecture unless this similarity is implied. Actually the arrangement of the trunk limbs and especially of their inner setal armature is totally different in the two cases. The mandible of *Nebalia* with its large, typically Malacostracan palp shows no similarity whatever to the mandible of any Branchiopod. The maxillules of the Branchiopoda might be compared to the proximal endite of the maxillule of *Nebalia*, but no Branchiopod maxillule bears a recurved palp. Finally, the maxillæ of the two types are about as different as any two Crustacean limbs can be. Unfortunately STORCH does not give any further details in support of his remarkable comparisons.

However, one important feature precludes any possibility of deriving the *Nebalia* mechanism direct from that of the Anostraca. In the latter the main food current passes

anteriorly (LUNDBLAD, 1920) along the mid-ventral food groove. In *Nebalia* it passes posteriorly. In advancing any hypothesis deriving one type of feeding mechanism from another functional continuity is essential, and this is impossible if it is attempted to derive the *Nebalia* type from the Anostracan type, for at one stage in the transition the food current would have to pass neither backwards nor forwards, and this, of course, would involve the non-functioning of either mechanism.

The similarities between *Nebalia* and a Mysid, as CLAUS pointed out, become much more significant when *Paranebalia* is considered. In this form the trunk limbs are not markedly foliaceous. The endopodites are not very flattened, but they terminate in a brush of long setae turned sharply back at right angles just as in *Nebalia*. The exopodites differ markedly from those of *Nebalia* and closely resemble those of a Mysid, or, in fact, any primitive Malacostracan. They commence with a large muscular basal joint and taper away distally in a many-jointed, whip-like limb fringed on either side with setae. *Paranebalia* thus forms in this respect a link between a primitive Malacostracan, e.g. a Mysid and *Nebalia*.

Now, *Hemimysis* and, as Miss MANTON and I hope to show shortly, all primitive Malacostraca possessed two separate methods of feeding, one for feeding on large particles and the other a filtering mechanism which resulted from their swimming activities. Certain Mysids took to burrowing in the mud and, in correlation, developed a large enveloping carapace and became the Cumacea. Parallel with this I believe that another group of Mysids, or else some other primitive Malacostracan group, also took to burrowing and gave rise to the Leptostraca. From the morphological standpoint this is quite possible when, as CLAUS pointed out, *Paranebalia* is taken into account. From the functional standpoint also I think it is quite feasible. Of the two feeding mechanisms at the disposal of this ancestral form the filter mechanism depended on the rotary swimming movements of the trunk-limb exopodites. Naturally the mud habitat would obviate the necessity of these swimming activities, and so, with their disappearance, the method of filter feeding would be discarded, and the ancestral *Nebalia* would have fed simply on large pieces of detritus picked up directly by its mouth-parts. The large carapace then developed probably as a protection for the supposed respiratory organs, the epipodites. This would not put the large food mechanism out of action, because even in a modern *Nebalia* the mandibular palps project beyond the carapace edges, but it must have led to an alteration in the mode of progression. The ancestral Mysid walked on its endopodites as does *Macromysis* nowadays. The carapace must have put these out of action as ambulatory limbs, and the oar-like action of the antennules developed in compensation. Now I pointed out earlier that this action of the antennules, in pushing the animal through the mud, must tend to suck mud particles into the anterior opening of the carapace. Thus, as a result of the burrowing habits, an irregular backwardly directed current entering the space over the mouth-parts would be established. The paddling action of the *Nebalia* limbs then developed to enhance this backwardly directed stream, and as a further adaptation the trunk limbs developed their foliaceous character.

The increased food stream brought more food to the mouth, consisting both of large particles and of particles too small to be dealt with by the mouth-parts, and a new filtering mechanism developed as a means of utilising this fine suspended food.

Thus, by combining the study of the structure of the limbs of *Nebalia* with a consideration of the way in which those limbs are used, I conclude that *Nebalia* is not, as HANSEN (1920, p. 75) states, the lowest among the Malacostraca, but is a form, highly specialised in correlation with its mud-living habits, that has evolved from some primitive Mysid-like Malacostracan.



If my views are correct, the filter mechanism of *Nebalia* represents an entirely new process involving a complete rearrangement of parts, but, while those parts may be homologous or "structurally continuous" with more primitive Crustacean limbs, the way in which those parts are used is "functionally discontinuous" with the ancestral mechanism. This can be taken as an example of Dollo's Law applied to functions. The primitive filtering mechanism disappeared, and with the re-establishment of a filtering method of feeding the original mechanism did not return, but an entirely new method was established.

I have already pointed out that *Paranebalia* leads on to *Nebalia*. While the setal armature is practically the same, the trunk limb of *Nebalia* is much more foliaceous than that of *Paranebalia*, and hence the filtering mechanism is probably more efficient. *Nebaliopsis* shows a development beyond *Nebalia*. The trunk limb of this form is simply a large lobed plate, all trace of the segmentation of the endopodite having disappeared. In its mouth-parts *Nebaliopsis* shows some interesting modifications. Firstly, the first trunk limb differs very markedly from the more posterior limbs, its proximal gnathobasic setæ being very well developed. The maxilla is very large and does not carry a heavy distal armature of setæ as in *Nebalia*. It looks very much like the proximal part of the first trunk limb. These two limbs armed with setæ point towards the mouth, and are probably the main gnathobasic structures. Correlated with this, the maxillule, especially the proximal endite, is very small. This character, together with the absence of distal setæ on the maxilla and the small size of the mandibular palp, suggest in my opinion that *Nebaliopsis* is entirely a filter feeder.

#### SUMMARY.

1. *Nebalia* is a mud-living form feeding on food particles filtered from a food stream produced by its foliaceous trunk limbs.

2. The food stream enters anteriorly and makes its exit at the posterior end of the carapace.

3. The current is produced by the oscillatory movements of the trunk limbs. The anterior limbs are the main inhalent pumps, the posterior being exhalent as well as inhalent. The exopodites and epipodites act as valves allowing water to pass out posteriorly and preventing water passing forwards.

4. The trunk-limb endopodites are armed along their inner edges with four rows of setæ. The first and third rows are hooked and those of successive limbs interlock, forming a continuous filter wall on either side of the median chamber between the limbs. The fourth form a row of comb setæ combing the food off the filter walls, and the second a row of brush setæ sweeping the food upwards towards the mid-ventral food groove. The proximal setæ of the first row are stout and are not hooked, and form a gnathobasic series pushing the collected food towards the mouth.

5. On the eighth trunk limb the fourth-row setæ are absent, and the third rows interlock, forming a wall preventing the entrance of water into the filter chamber posteriorly.

6. On the first trunk limb the first-row setæ are not hooked, but two groups towards the base of the limb are very stout and function in pushing large food particles directly on to the mouth-parts.

7. The proximal endites of the maxillules and maxillæ both point between the bifid lower lip towards the mouth. The distal endites bite together in the transverse plane.

8. The mouth-parts, both structurally and in their method of functioning, closely resemble those of a Mysid.

9. From a comparison with *Paranebalia* it is suggested that *Nebalia* evolved from a Mysid, or some other primitive Malacostracan possessing a feeding mechanism similar to that of *Hemimysis*, that took to mud-living habits. The foliaceous limbs are in no way primitive, but evolved from typical biramous Malacostracan limbs in connection with the new method of filter feeding.

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XVI.—Air-Bladder and Lungs: A Contribution to the Morphology of the Air-Bladder of Fish. By Frances M. Ballantyne, B.A., Department of Zoology, University of Glasgow. (With Thirty-seven Figures.)\* Communicated by Professor J. GRAHAM KERR, F.R.S.

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INTRODUCTION.

In view of the frequent appearance, even in technical literature, of the old-fashioned idea that the lung of the tetrapod has evolved out of the air-bladder of fish, further work on the morphology of the air-bladder seems desirable. The theory of an air-bladder origin of the lung was brought forward by BOAS, who based his view on purely theoretical arguments, which have, however, not found support in the facts brought to light by the advance of our knowledge of the embryology of the more archaic vertebrates.

It is generally accepted that there is no air-bladder in the Elasmobranchs, though, according to the observations of MIKLUCHO-MACLAY (25), there is a very transitory rudiment in the young stages of *Galeus*, *Mustelus*, and *Acanthias*. PAUL MAYER (24), in dealing with MIKLUCHO-MACLAY's paper, states that the supposed air-bladder rudiment is simply the early stage of one of three large and distinct glands present in the adult, the other two of which are ventral in position. This seems conclusive, but in regard to his criticisms of the rest of MIKLUCHO-MACLAY's paper, I do not think his reasoning is sound. His only argument against the existence of the rudiment in *Galeus* and *Acanthias* is that he has not found it in much older specimens. But if the air-bladder is only a vestigial organ in these fish, one would not expect to find it persisting until the later stages of development. Further investigation might be of value, especially in view of the widespread tendency of the air-bladder to become reduced even in such primitive fish as *Acipenser* and *Scaphirhynchus*, not to mention the more highly specialised benthotic Teleosts.

The air-bladder is a well-developed organ in most Teleosts and in the Dipnoi, though its adult form varies very considerably in different groups. In the Dipnoan *Lepidosiren* and *Protopterus*, and in the Crossopterygian *Polypterus*, there are two well-developed lungs opening ventrally into the alimentary canal. In *Ceratodus* there is a single lung, which, though lying dorsal to the alimentary canal, yet communicates with the ventral wall of the oesophagus, its pneumatic duct passing round the right side of the canal. In the Teleosts, the air-bladder is a dorsal sac, opening in the Physostomes into the alimentary canal either dorsally or laterally, and in the Physoclisti, having in the adult no such communication with the alimentary canal.

As regards the evolutionary history of the organ, there have been two main theories; one of which regards the air-bladder as an organ *sui generis*, whereas the other traces the homology of the air-bladder with the lungs of other vertebrates. The first of these theories was supported by WIEDERSHEIM (40). It was largely based upon his observations upon Dipnoi which have been proved to be erroneous, and the view can no longer be entertained in the light of our further embryological knowledge.

The second of the two theories is due especially to SAGEMEHL (36), who based his view on the great variability in position of the glottis in different fishes, especially in the Characinidæ. Professor GRAHAM KERR's (19) results, on *Polypterus* and the Dipnoi, make it impossible to avoid accepting this view. The early stages of development of the organ in *Polypterus* and

\* I desire to thank the Carnegie Trustees for the Universities of Scotland for a grant in aid of the cost of the illustrations.

the Dipnoi, are identical with those of a typical lung. In *Polypterus*, which in this respect is more archaic than the Dipnoi, the two lungs are not of equal size, the larger right lung assuming a dorsal position where it is not balanced by the left lung. This posterior part of the right lung is supplied by both the right and the left vagus nerves, the left nerve crossing over dorsal to the alimentary canal. This is very important, since it foreshadows the crossing of the nerves in the Dipnoi, a fact which caused great difficulty in understanding the arrangement of the lungs in this group.

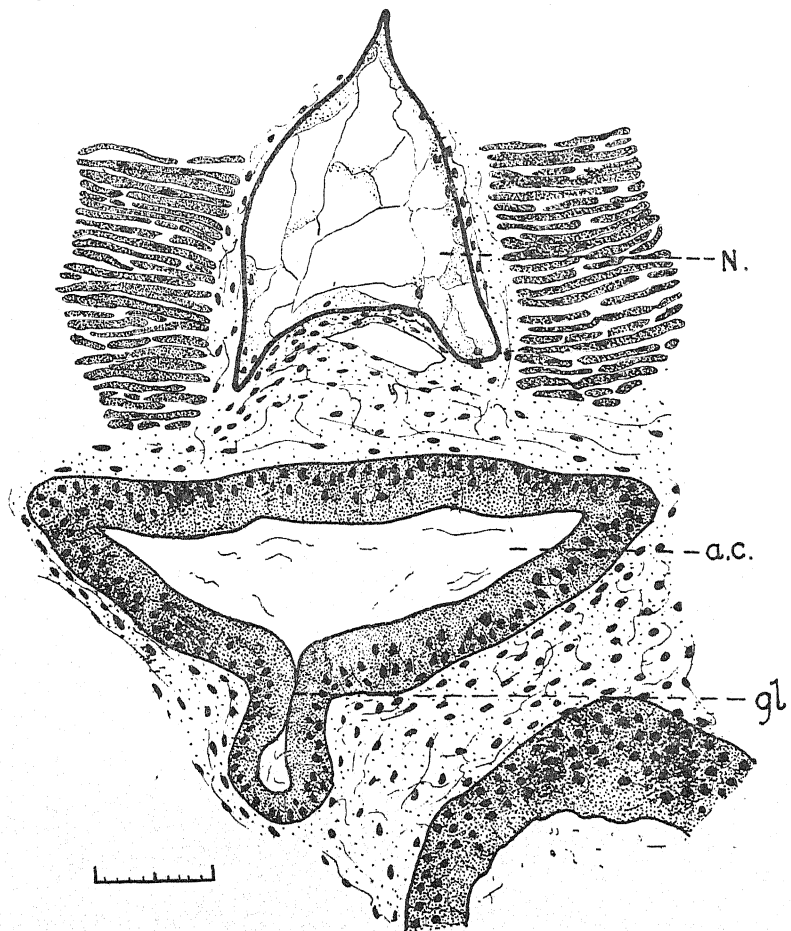


FIG. 1. Lung rudiment of *Ceratodus* at an early stage when the lung extends back and towards the right only.

Lettering for all Text-figs.: B, brain; N, notochord; a.b, air-bladder; a.c, alimentary canal; a.h, anterior horn of air-bladder; c.a, coeliac artery; d.a, dorsal aorta; gl, glottis; k, kidney; l, liver; l.l, left lung; l.p.a, left pulmonary artery; l.p.n, left pulmonary nerve; p.a, pulmonary artery; ph, pharynx; r.l, right lung; r.p.a, right pulmonary artery; r.p.n, right pulmonary nerve; sp.c, spinal cord.

Each division of scale, except in Fig. 6 D, represents 0.01 mm.

In the Dipnoi the right nerve and the pulmonary arteries show clearly that the lungs have travelled round the right side of the alimentary canal to take up their adult position, and the apparent contradiction provided by the crossing of the left pulmonary nerve dorsal both to the alimentary canal and to the right nerve, is explained when the crossing is found to be already present in an earlier evolutionary stage. Probably this crossing is due to short-circuiting of nerve impulses.

Another important fact established by Professor GRAHAM KERR's (19) work on the Dipnoi, is that the symmetrical lungs of *Lepidosiren* and *Protopterus* pass through an asymmetrical "Polypterus stage" in the course of their development.

The object of this paper is to review and extend observational knowledge bearing on the question, by studying in detail the air-bladder as it exists in the adult and the embryonic stages of the more primitive types of existing fish. The material used has consisted of embryos and adults of *Amia*, *Lepidosteus*, *Acipenser*, and *Gymnarchus*, while adults of *Scaphirhynchus* and embryos of *Ceratodus* and *Callichthys* have also been examined.

#### CERATODUS.

As has been stated above, in *Ceratodus* the whole lung lies dorsally, though the pneumatic

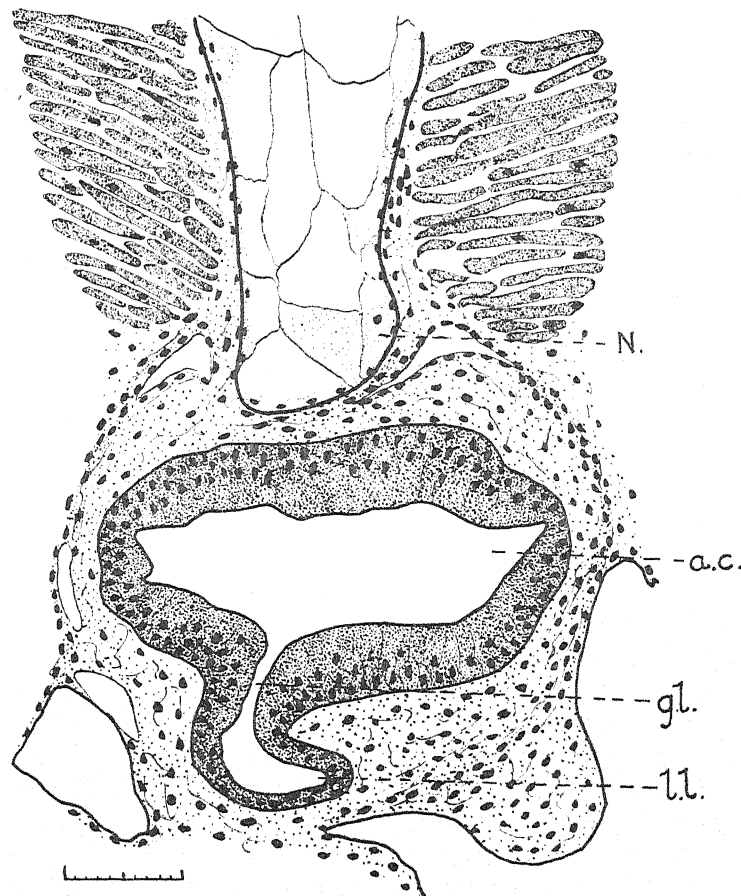


FIG. 2. Lung rudiment of *Ceratodus*, showing the vestigial left lung; 15 mm. embryo.

duct passes round the right side of the alimentary canal to open into the ventral wall of the oesophagus. There is only one lung in the adult, and the left lung is only vestigial in the embryo. As NEUMAYER (28) has described, the lung first appears as a small, ventrally directed evagination of the ventral wall of the alimentary canal. This grows ventrally and caudally at first, and then begins to turn to the right and upwards round the alimentary canal. The lung rudiment at first passes straight down ventrally and then turns almost at a right angle and extends back caudally. At a slightly later stage the ventral end of the pneumatic duct, if we may so call the anterior vertical part of the lung rudiment, becomes broadened out towards the left side. This is figured both by GREGG WILSON (41) and by NEUMAYER, and the latter says that this left process of the widened-out end of the primitive lung cavity may represent the rudiment of the left lung.

In the sections which I have examined, there is no trace of this left process in the earliest



stages (fig. 1). The tip of the rudiment turns backwards and upwards round the right side of the canal. It is just where the turn occurs, and when already the lung has grown some

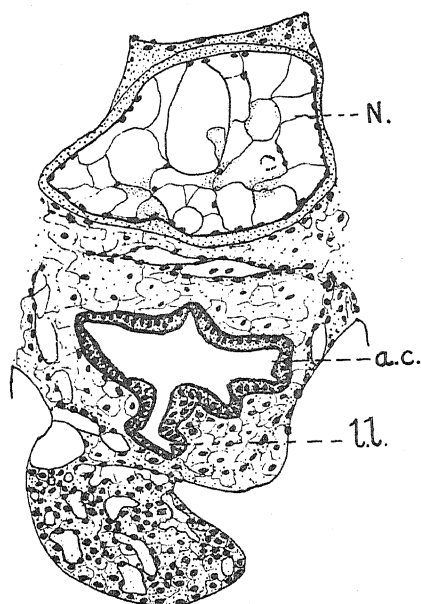


FIG. 3.—The same; 18 mm. embryo. A, glottis and vestigial left lung.

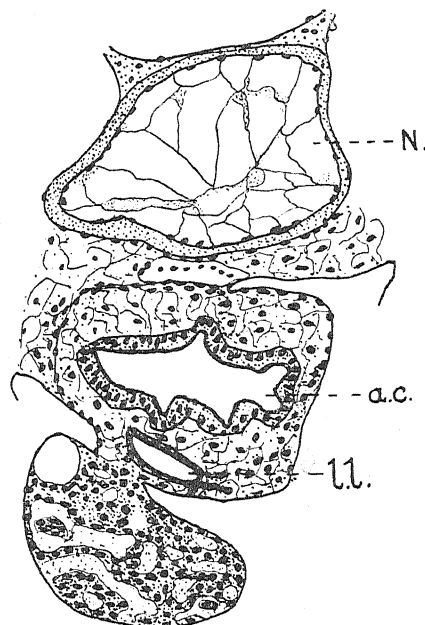


FIG. 3.—B, left lung merging with main right lung.

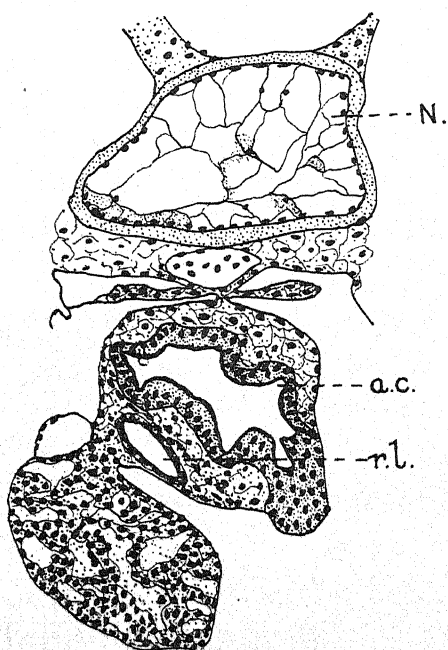


FIG. 3.—C, showing the rotation of the lung round the right side of the canal.

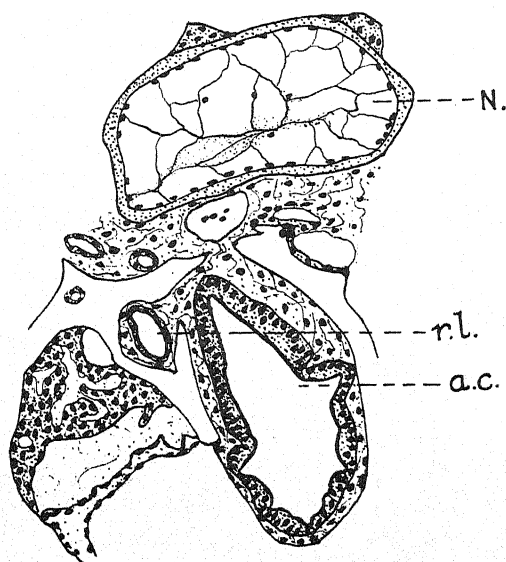


FIG. 3.—D, showing further rotation of the lung round the right side of the canal.

distance backwards and towards the right, that the minute left lung appears (fig. 2). In an embryo of 15 mm. length the left lung has attained its maximum size, and after that rapidly becomes merged in the main or right lung (fig. 3). As in the other Dipnoi, the lung of *Ceratodus*

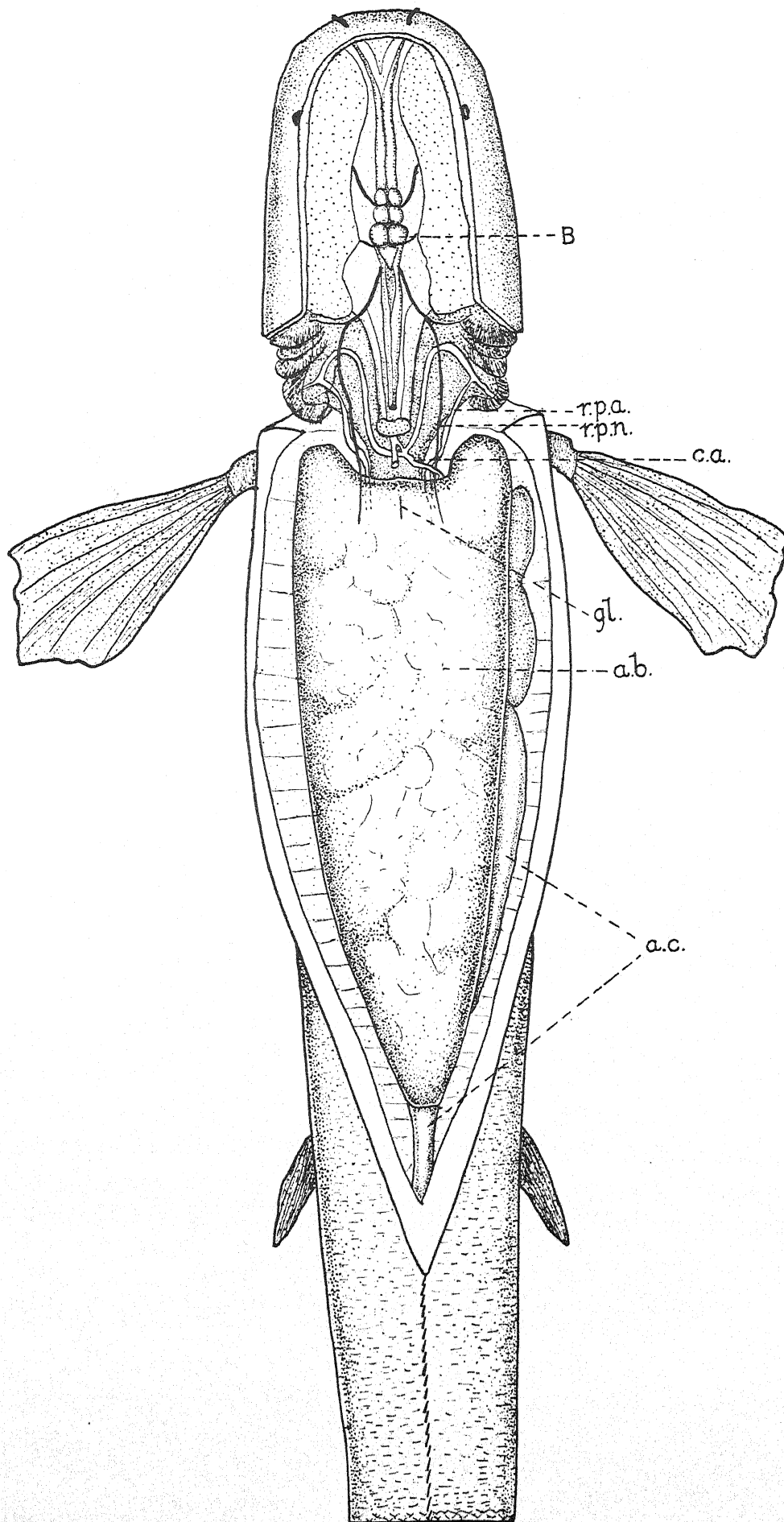


FIG. 4.—Dorsal dissection of adult *Amia*, showing air-bladder and its nerves and arteries.

is supplied with blood from the sixth aortic arch by normal pulmonary arteries, which by their course show clearly how the lung has travelled round the œsophagus, the left artery

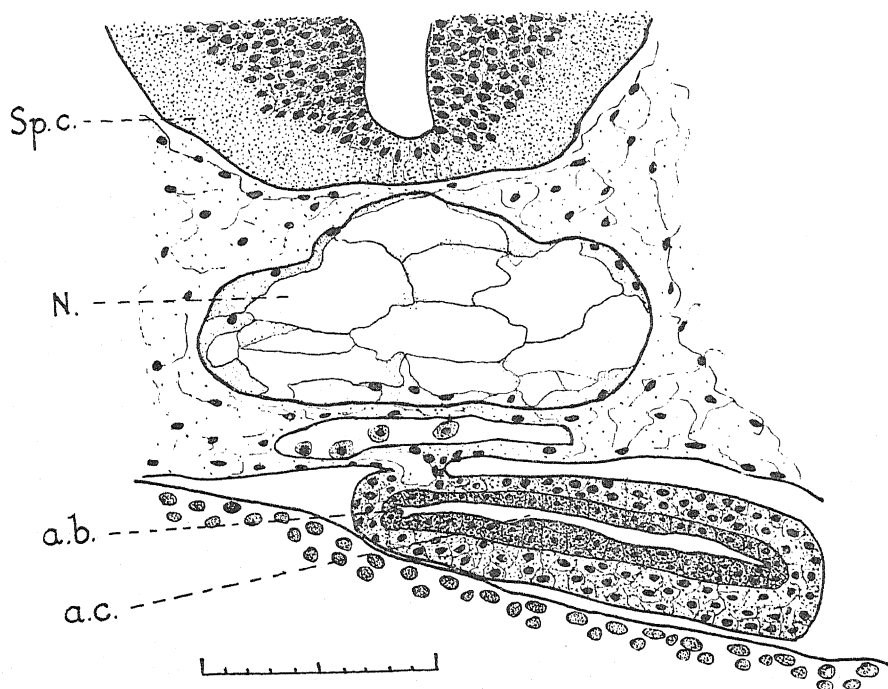


FIG. 5.—Transverse sections through developing air-bladder in *Amia*. A, earliest stage of air-bladder; 7 mm. embryo.

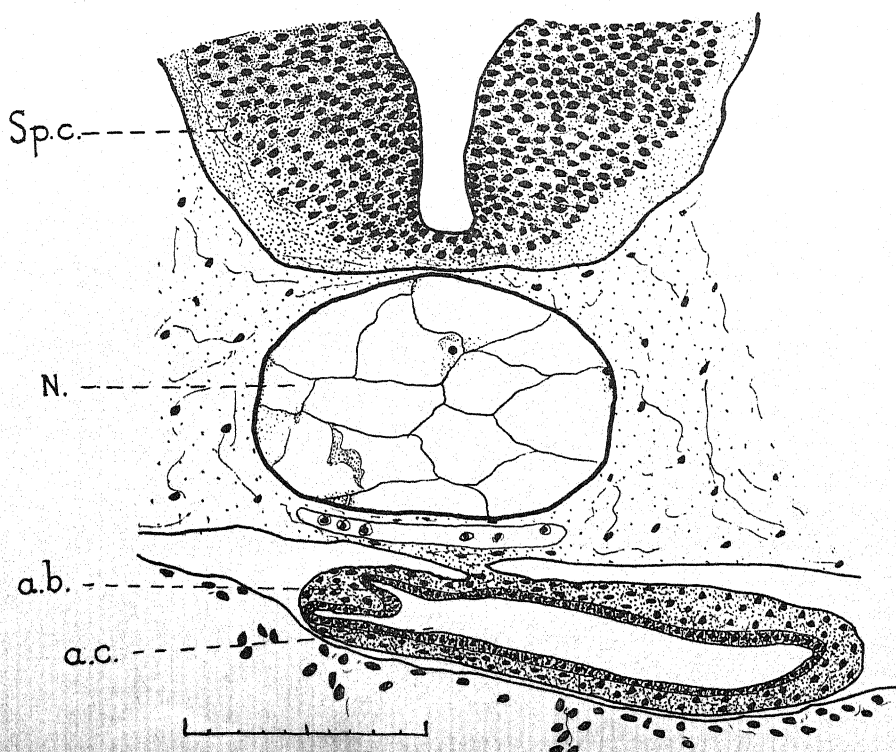


FIG. 5.—B, a slightly later stage; 7 mm. embryo.

passing round ventral to the alimentary canal to supply the ventral side of the lung. The nerves are typical pulmonary branches of the vagus of each side. The left nerve crosses



dorsal to the alimentary canal and to the right nerve as in other Dipnoi, but, as shown by Professor GRAHAM KERR (18), this is to be regarded as a secondary arrangement.

#### AMIA.

The next probable step in the evolutionary history of the air-bladder is illustrated by *Amia*. In *Amia* (fig. 4) the air-bladder of the adult is a large, very vascular sac, lying in the dorsal mesentery and extending from the level of the pectoral fins almost to the end of the body cavity. It is distinctly bilobed in front and tapers slightly towards the posterior end. The walls are membranous with a complicated network of blood-vessels, giving a spongy appearance to the organ. The short pneumatic duct leads from the front of the air-bladder to the glottis situated in the mid-dorsal wall of the alimentary canal, a little behind the last gill cleft. The blood supply is by typical pulmonary arteries from the sixth aortic arch of

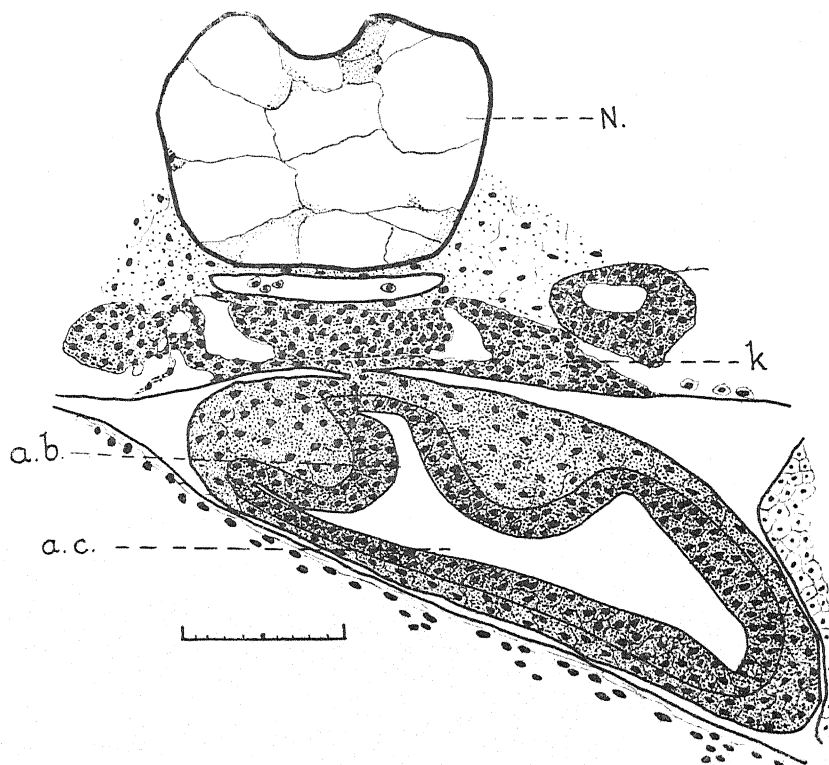


FIG. 5.—C, 9 mm. embryo.

each side. This artery (r.p.a.) is given off at the bend of the gill arch, passes inwards under the cardiac branch of the vagus, and then turns tailwards along the outer side of the pulmonary branch (r.p.n.) of the vagus nerve. Just after entering the body cavity, the artery bends under the nerve so that it enters the air-bladder internal, and somewhat ventral, to the nerve. Both artery and nerve enter the bladder on its ventral side, on either side of the pneumatic duct. The coeliac artery (c.a.) crosses dorsal to the artery and nerve on the right side, as one would expect it to do if the air-bladder had been originally ventral. The veins run alongside the artery and nerve until they enter the posterior cardinal vein. In front of this, for some distance, the artery and nerve are closely pressed against the wall of the posterior cardinal vein.

In development the air-bladder of *Amia* first appears in an embryo of about 7 mm. length (fig. 5, A), as a very minute pocket of the right side of the dorsal wall of the alimentary canal,

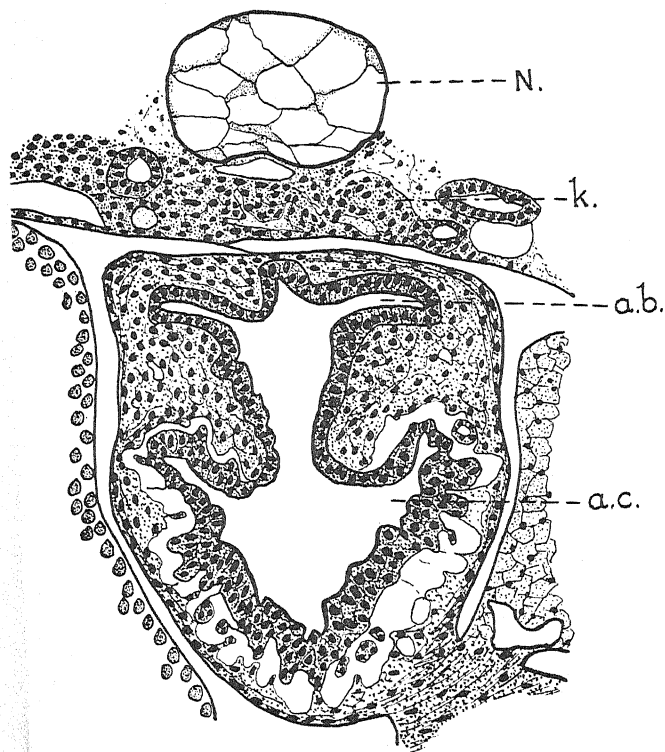


FIG. 5.—D, 12 mm. embryo.

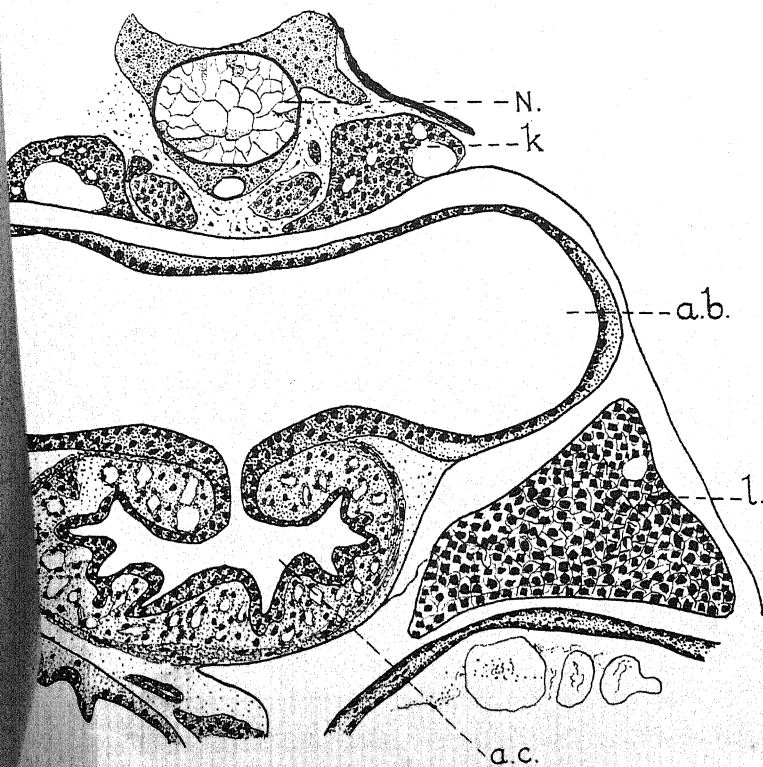


FIG. 5.—E, 19 mm. embryo.

0.1 mm.

FIG. 6

well to the right of the mesentery. PIPER (29) describes the first rudiment as mid-dorsal, but his figure shows the opening a little to the right with the tip still further over to the right. This is a later stage than that represented by the 7 mm. embryo.

The rudiment gradually increases in length, becoming an open groove in the wall of the canal, and by rotation of the cesophagus, it tends to become mid-dorsal in position (fig. 5, C). The simple groove becomes T-shaped, as seen in transverse section (fig. 5, D, E), and the left branch of the T grows back as a tubular sac lying dorsal to the alimentary canal, and a little to the left side of the median plane.

Gradually the groove becomes closed off from the alimentary canal from behind forwards, and the cavity of the air-bladder becomes larger and the right branch of the T-shaped part merges with the left to form the long vascular sac of the adult, lying mid-dorsally in the body cavity (fig. 6, A-D). This process is comparable with that by which the left lung rudiment in *Ceratodus* gradually disappears into the general contour of the persistent right lung; for in comparing the dorsally placed sac in *Amia* with the typical, ventral lungs, it must be borne in mind that the

left side of the air-bladder of *Amia* represents the morphologically right side of the lungs.

Therefore in *Amia*, the air-bladder may be considered as the persistent right lung as in *Ceratodus*. Here, however, the rotation of the alimentary canal has brought the glottis

round to the right side of the dorsal wall, when the rudiment first appears, and by further rotation to the mid-dorsal line in the adult. It is of interest to note that in the embryos of *Amia* and other Ganoids the alimentary canal hangs free in the body cavity, and is therefore free to rotate; whereas in the embryo of *Ceratodus*, the cesophagus is firmly embedded in connective tissue.

Another point which emerges from a study of serial sections and which deserves to be emphasised is that the position of the stomach, well down on the left side, is such as would seriously interfere with the left lung were one present. In the absence of a similar handicap in the case of the right lung, we have a factor which probably played an important part in initiating the predominance of the right lung over the left, which is seen in the evolutionary history of the air-bladder.

The fact that the arteries are not crossed in *Amia* is explained when it is noted that the air-bladder is already a large, well-developed sac when the last gill cleft is first opened. The first appearance of the air-bladder is in a 7 mm. embryo, but the gill clefts are completely developed for the first time in a 12 mm. embryo, in which the air-bladder is already approximately 1 mm. long. This is the first stage at which the arteries

can be traced, so that the principle of economy of tissue would naturally account for the left artery taking a short cut to the left side of the air-bladder.

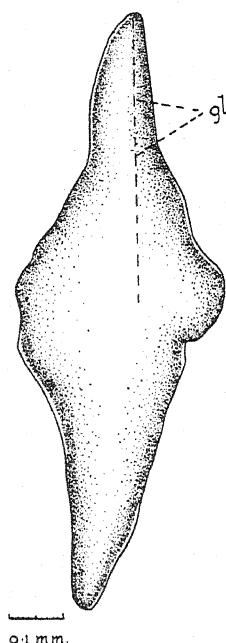
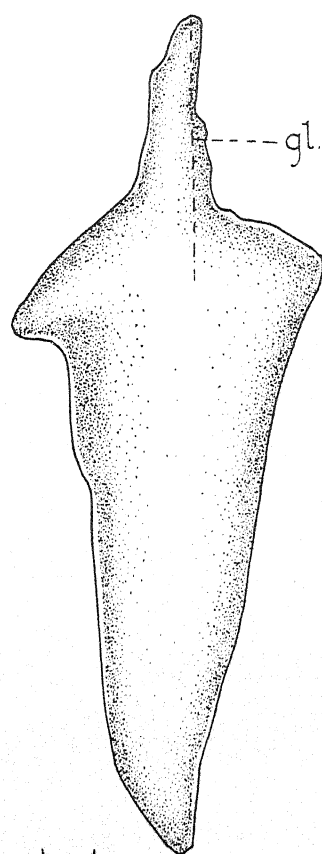


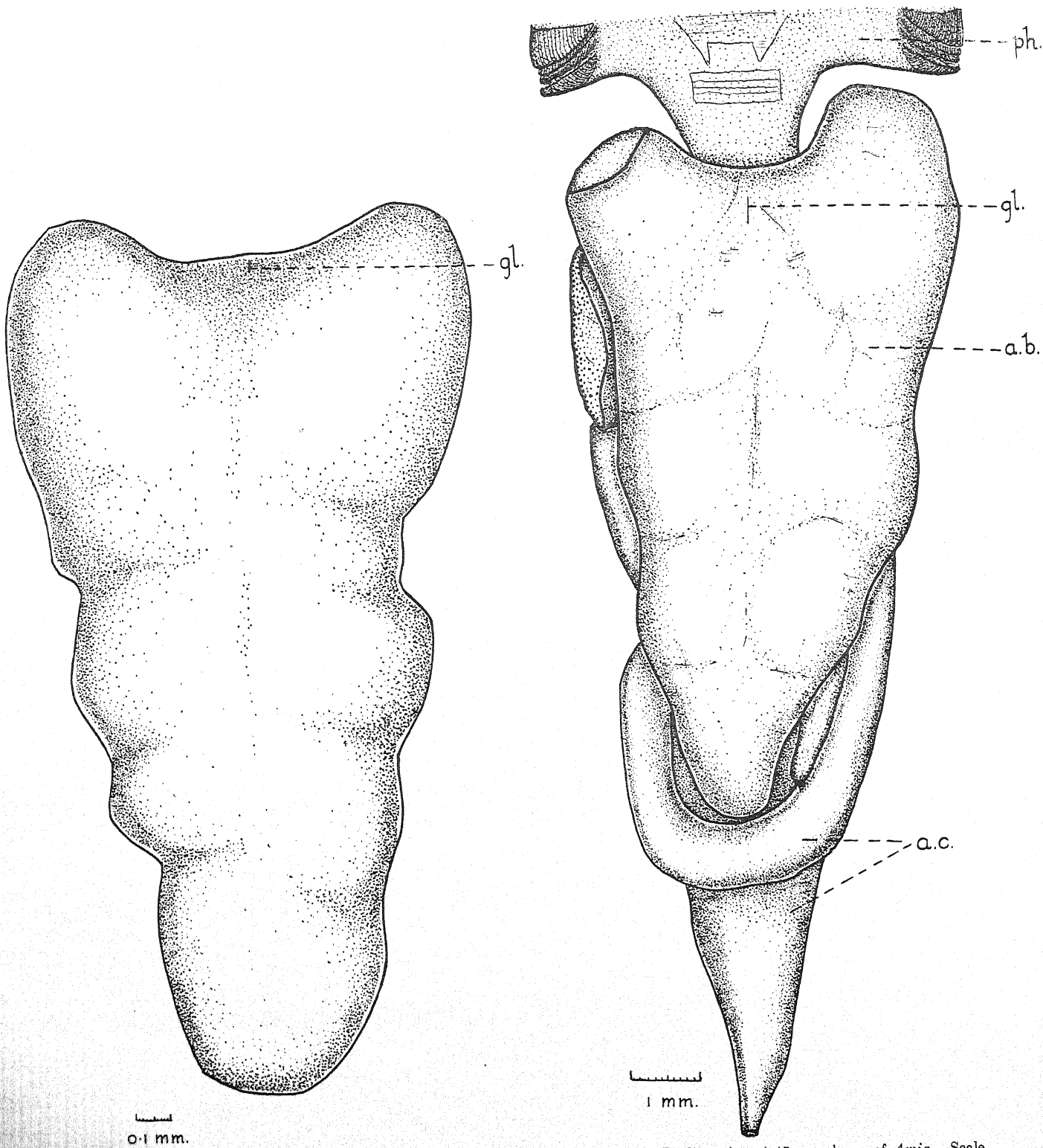
FIG. 6. — Reconstructions from horizontal sections of air-bladder of *Amia*, A, 10 mm. embryo.



0.1 mm.

FIG. 6.—B, 11 mm. embryo.





0.1 mm.

FIG. 6.—C, 20 mm. embryo

FIG. 6.—D, dissection of 45 mm. larva of *Amia*. Scale much smaller than A, B, C.

The nerves (fig. 7) also go straight to the same side of the air-bladder—left nerve to left side—but the condition in *Polypterus*, of the nerves to the posterior part of the right lung, foreshadows this arrangement. As already noted, the cœliac is dorsal to the right artery and nerve, thus showing a trace of a more primitive arrangement.

#### LEPIDOSTEUS.

Another step towards the Teleostean air-bladder is shown in *Lepidosteus*. As in *Amia*, the air-bladder is typically lung-like; the vascular network of the walls is very intricate, and is supplemented by blood-vessels running across the cavity of the sac and forming pockets at the sides of the main cavity. In the adult, the glottis is mid-dorsal, but somewhat further forward than in *Amia*, and opens immediately behind the pharynx. The nerves are pulmonary branches of the vagus on either side; the blood-supply, however, is not from the sixth aortic arch, but from numerous arteries coming straight from the dorsal aorta. The veins also are numerous and enter the posterior cardinal veins.

According to MAKUSCHOK (22), the air-bladder appears first in an embryo of about 8 mm. length, as a mid-dorsal diverticulum of the posterior part of the œsophagus. The, at first, small and circular glottis extends forwards, giving the appearance of an immediately post-pharyngeal origin for the air-bladder.

In embryos of 12, 15, and 18 mm. length, which I have examined, the lung is well developed and extends through almost the whole length of the body cavity. It has distinct processes to the right and left anteriorly, reminding one of the T-shaped part of the air-bladder of *Amia*. Reconstructions from horizontal sections of

these three stages seem to indicate that the rudiment is at first a simple sac, and that the processes to right and left develop later. In the 12 mm. embryo there is a long, straight sac with, at the anterior end, a small process on the left side. In the 15 mm. specimen this process has become much larger, and another process to the right has appeared. In the 18 mm. embryo the left pocket is disappearing into the general contour of the lung, the right process being still distinct. MAKUSCHOK only figures earlier stages than this.

In embryos of 11 and 10 mm. length, transverse sections show that the air-bladder, at the anterior end near the pharynx, is a mid-dorsal groove in the wall of the apparently solid œsophagus. As the cavity of the œsophagus appears farther back, the cavity of the groove-like rudiment of the air-bladder also appears, and finally the groove becomes cut off from the alimentary canal and extends for some distance as a tubular sac, lying mid-dorsally in the body cavity. This is very like a corresponding stage in *Amia*.

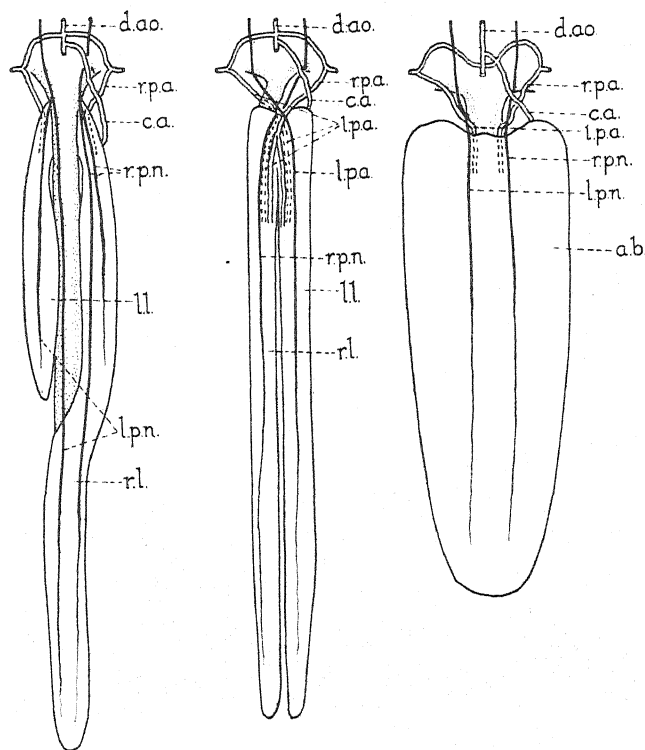
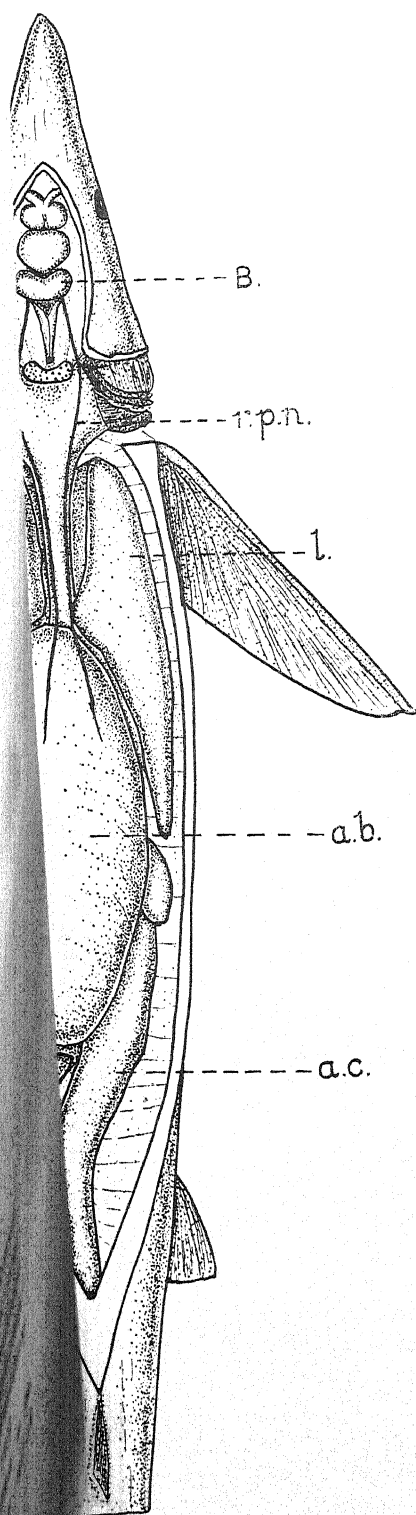


FIG. 7.—Diagram to show nerves and arteries of the lungs of:  
A, *Polypterus*. B, *Lepidosiren*. C, *Amia*.

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Adult *Acipenser*, showing air-bladder and its nerves.

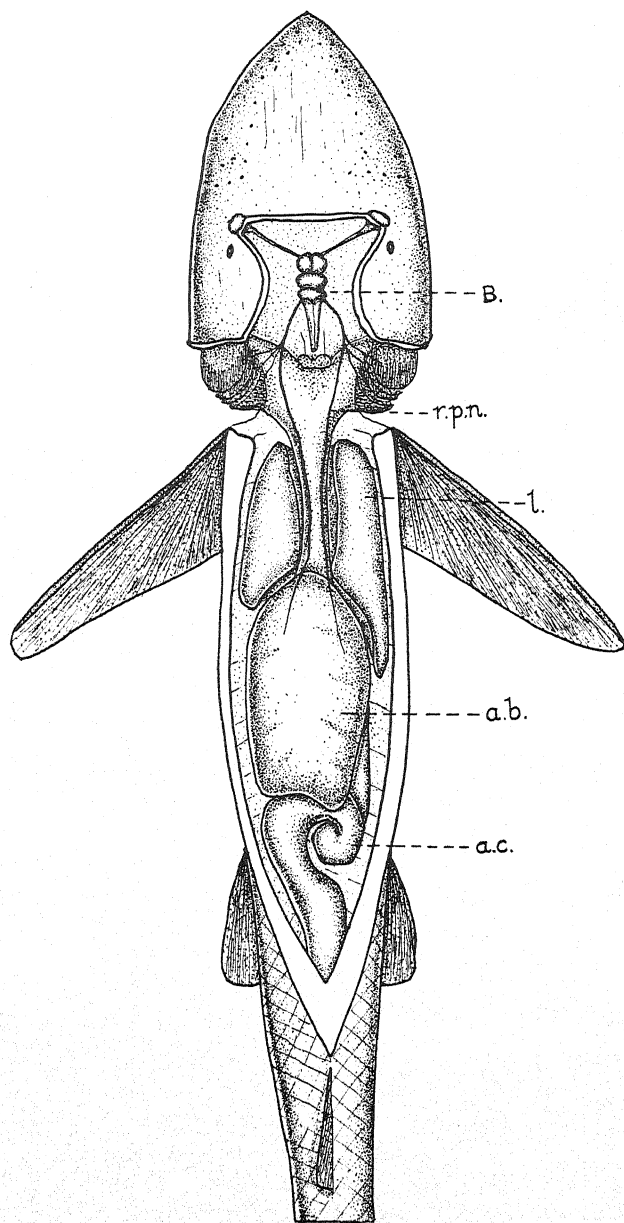


FIG. 9.—Dorsal dissection of *Scaphirhynchus platyrhynchus*, showing air-bladder and its nerves.

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In the sturgeons, as we might expect from their ground-feeding habits, the air-bladder is in a very much reduced condition, and probably represents a stage when both the respiratory and the hydrostatic functions have degenerated owing to life at the bottom of the water. The air-bladder lies much farther back in the body cavity than in *Amia* and *Lepidosteus*, and the glottis opens into the anterior end of the stomach (fig. 8).

#### ACIPENSER AND SCAPHIRHYNCHUS.

MACALLUM (21), in describing the alimentary canal of *Acipenser*, states that, from the histological structure of the walls of the canal, the œsophagus may be said to extend just posterior to the opening of the pneumatic duct, so that here also the air-bladder is in reality a diverticulum of the œsophagus.

According to RAUTHER (30), the size and development of the air-bladder varies very much

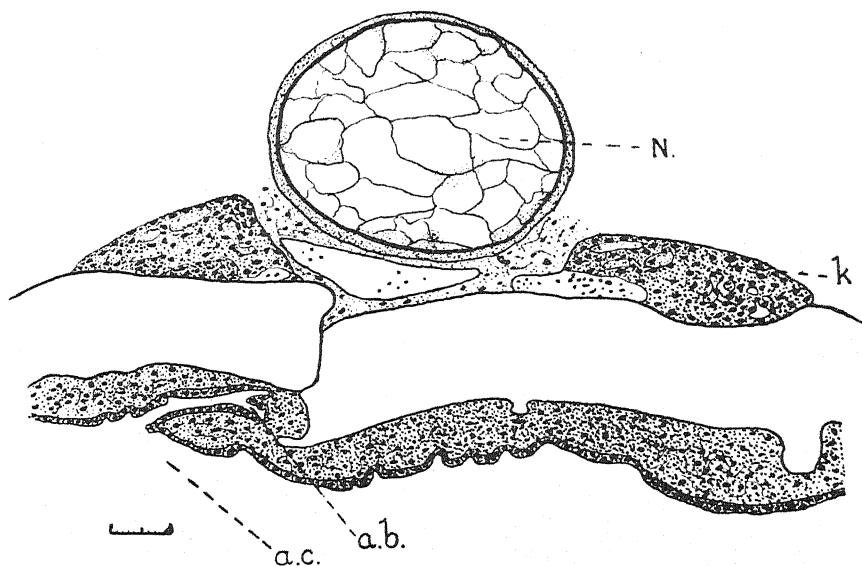


FIG. 10.—Earliest stage in development of air-bladder of *Acipenser*; 28 mm. embryo.

in different species of *Scaphirhynchus*. In *S. fedtschenkoi*, it is only a small sac with a rudimentary cavity opening into the hinder part of the œsophagus, although in *S. rafinesquei* it is a long sac with a large pneumatic duct. In *S. platyrhynchus* (fig. 9), specimens of which I have dissected, it is a fairly large membranous sac with a curious, tough, fibrous lining to the dorsal and lateral walls. It lies dorsally in the middle of the body cavity.

In development the air-bladder in *Acipenser* does not appear until late—another step in the process of degeneration. The very first rudiment is seen in an embryo of 28 mm. length (fig. 10), where it is a diverticulum of the lining of the alimentary canal. The opening is well over to the right side, and the tip of the diverticulum, which is directed towards the left, is distinctly bilobed. This diverticulum causes the outer wall of the alimentary canal to bulge very slightly. In an embryo of 30 mm. length (fig. 11, A), the air-bladder rudiment is a very small pouch on the proximal part of the stomach. In a specimen of this size the alimentary canal is fully formed and has reached its adult condition except in size. The air-bladder rudiment is nearly mid-dorsal and is a simple sac. In further stages it increases in size, especially in length, until it attains its adult structure (fig. 11, B-C).

## GYMNARCHUS.

The development of the air-bladder in *Gymnarchus* is of special interest for the light it throws upon the method by which the change has occurred from the normal pulmonary blood supply to that direct from the coeliac artery or the dorsal aorta. In the embryo the pulmonary artery originates from the fused fifth and sixth aortic arches of the left side, those of the right side forming the coeliac artery. Later, the origin of the pulmonary artery becomes shifted on to the aorta just in front of the coeliac, the fused fifth and sixth arches of each side

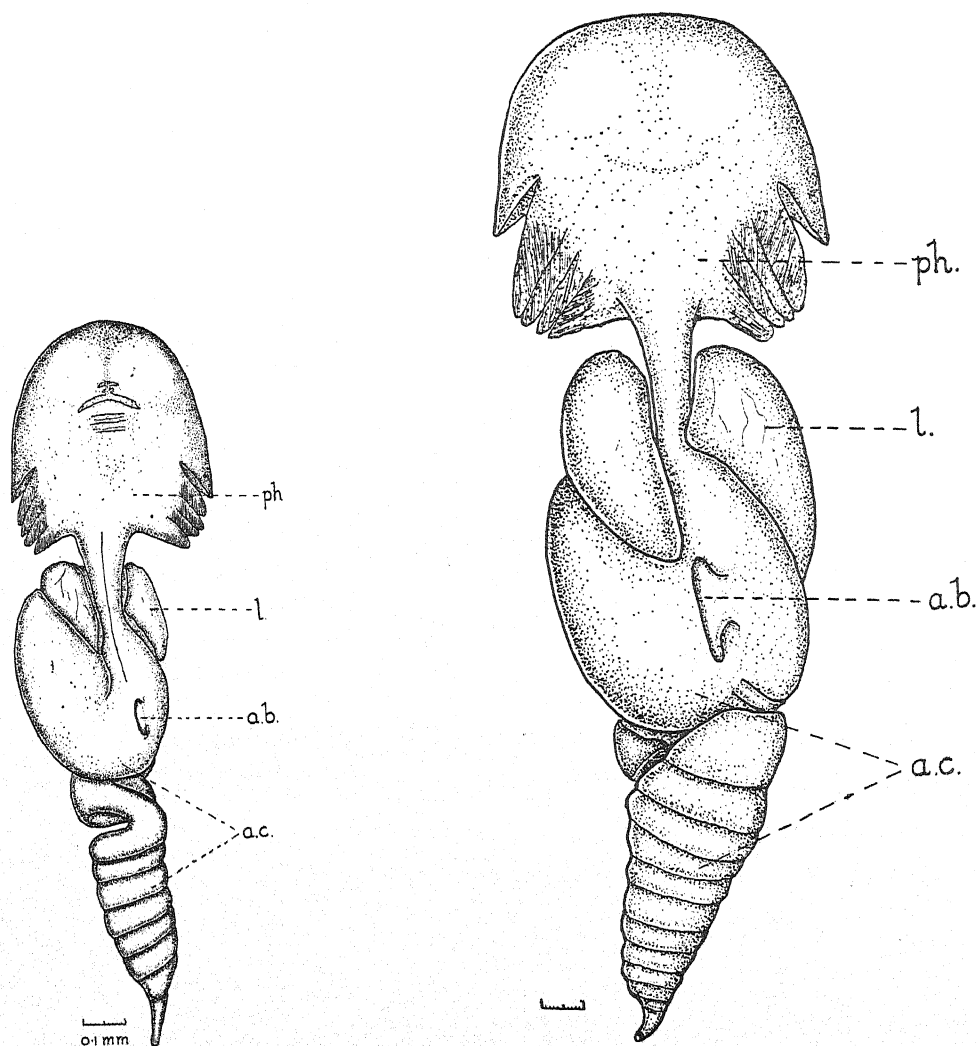


FIG. 11.—Dissections of the alimentary canal and the air-bladder rudiment of *Acipenser*:  
A, 30 mm. embryo. B, 50 mm. embryo.

coming together into the dorsal aorta. In the adult the pulmonary and the coeliac arteries are anastomosed at their origin from the dorsal aorta. It may be noted that in *Amia* the coeliac comes off from the junction of the sixth arches before they enter the aorta. In *Gymnarchus* there is only one artery to the air-bladder, and one vein coming from it to enter the posterior cardinal vein.

In *Gymnarchus* the air-bladder rudiment first appears in an embryo five days old (fig. 12, A) as a small diverticulum of the dorsal wall of the alimentary canal. The rudiment appears to be very slightly to the left of the mid-dorsal line, but I think this is probably due to the

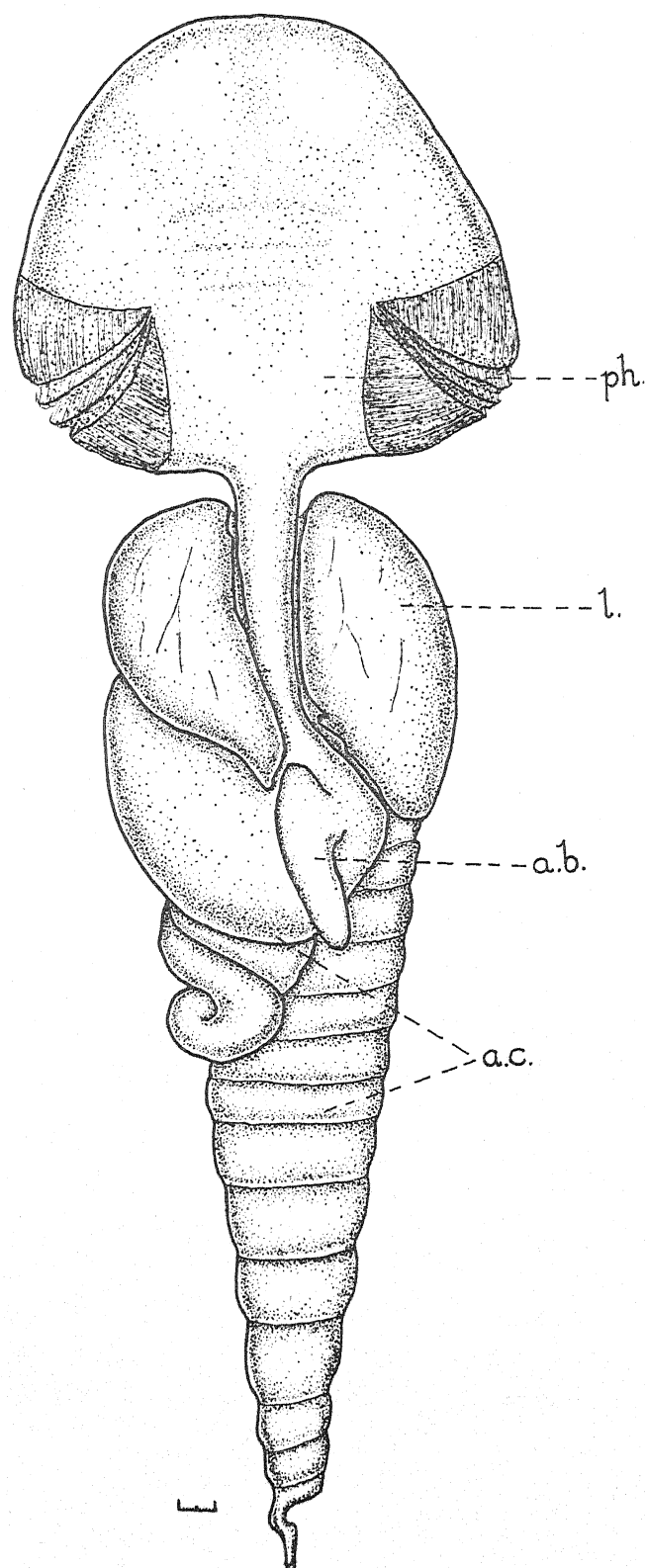


FIG 11.—C, 95 mm. embryo.



whole body of the embryo being twisted over to the right in the specimen sectioned. At this stage the embryo is still within the egg-membrane, and the whole of the head and anterior part of the body is lying on its right side. This twisting tends to obscure the exact topography of the organs, but the lung rudiment is, I think, approximately mid-dorsal. In a 6-day embryo the rudiment is deeper and forms a short groove in the wall of the canal. It is mid-dorsal as regards its relations to the notochord and the nerve cord, but is now well over to the left of the dorsal wall of the somewhat flattened alimentary canal, and is tilted over to the right (fig. 12, B-E). Reconstructions of horizontal sections of 7-day embryos show that the rudimentary air-bladder bulges well over to the right from the pneumatic duct and extends forwards and towards the middle line, and later, in a 15 mm. embryo, backwards also (fig. 13). In this 15 mm. embryo the duct is bent well over to the right so that the whole organ is dis-

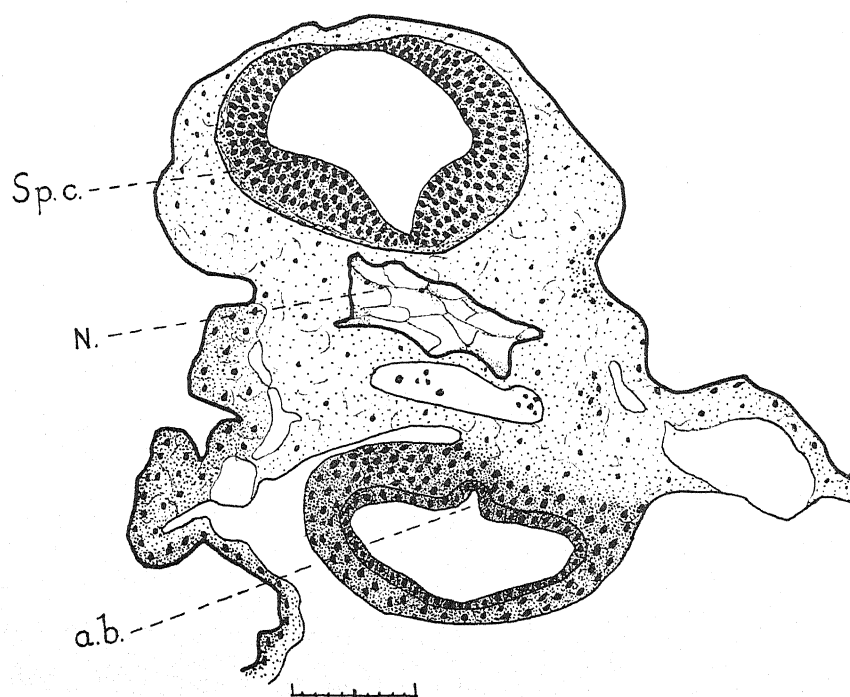


FIG. 12.—Transverse sections through the glottis of the developing lung of *Gymnarchus*:  
A, in 5-day embryo.

tinctly to the right of the body cavity. In an 18 mm. (8-day) embryo the organ has greatly developed. The anterior portion is, at its origin from the duct, well to the right, but further forwards it has assumed a central position and its anterior end is bifurcated, the two branches growing forward and somewhat to the sides. The portion posterior to the duct is very much enlarged and is also much nearer the mid-dorsal line than before. Already the cavity is becoming complicated by localised bulgings of the wall, so as to form intercommunicating chambers. In 9- and 10-day embryos the anterior horns of the air-bladder have reached the neighbourhood of the otocyst, and their stems are becoming reduced in diameter. The posterior or main portion of the air-bladder has a larger number of branching cavities than in earlier stages. The alimentary canal, which at earlier stages had a distinct and open cavity, is now almost solid, though the lumen of the air-bladder and its duct are not closed.

A reconstruction from horizontal sections of the air-bladder in an 11-day embryo, 34 mm. long (fig. 13, C), shows the curious arrangement of the cavities. The pneumatic duct now leads straight back into a long, tubular cavity which gives off side branches all round. This

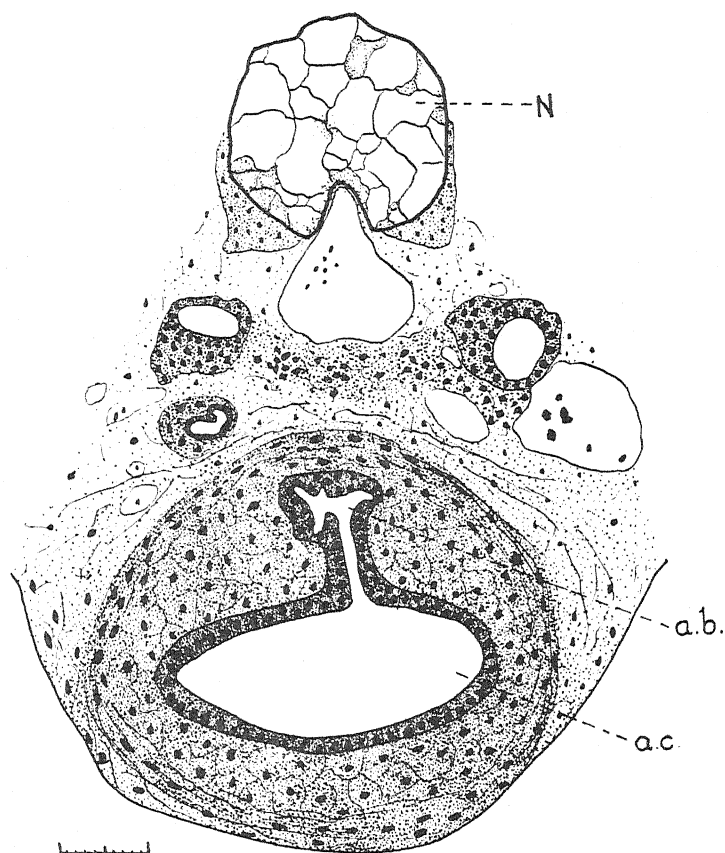


FIG. 12.—B, in 7-day embryo.

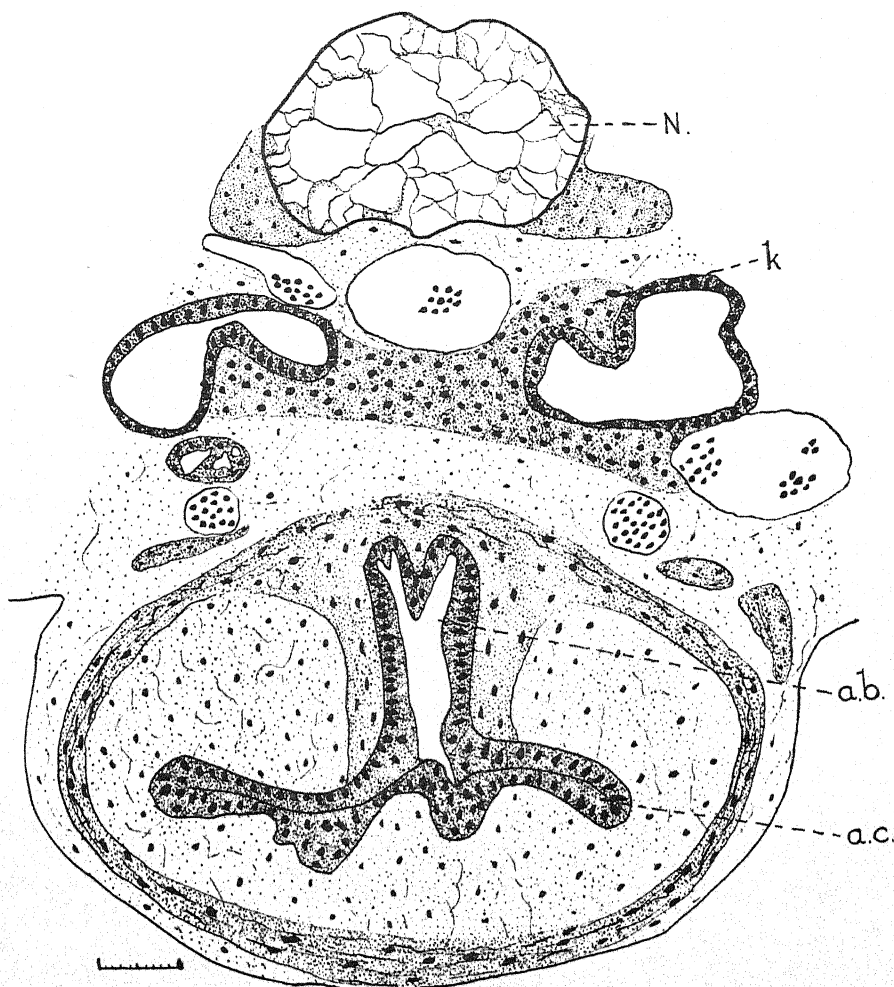
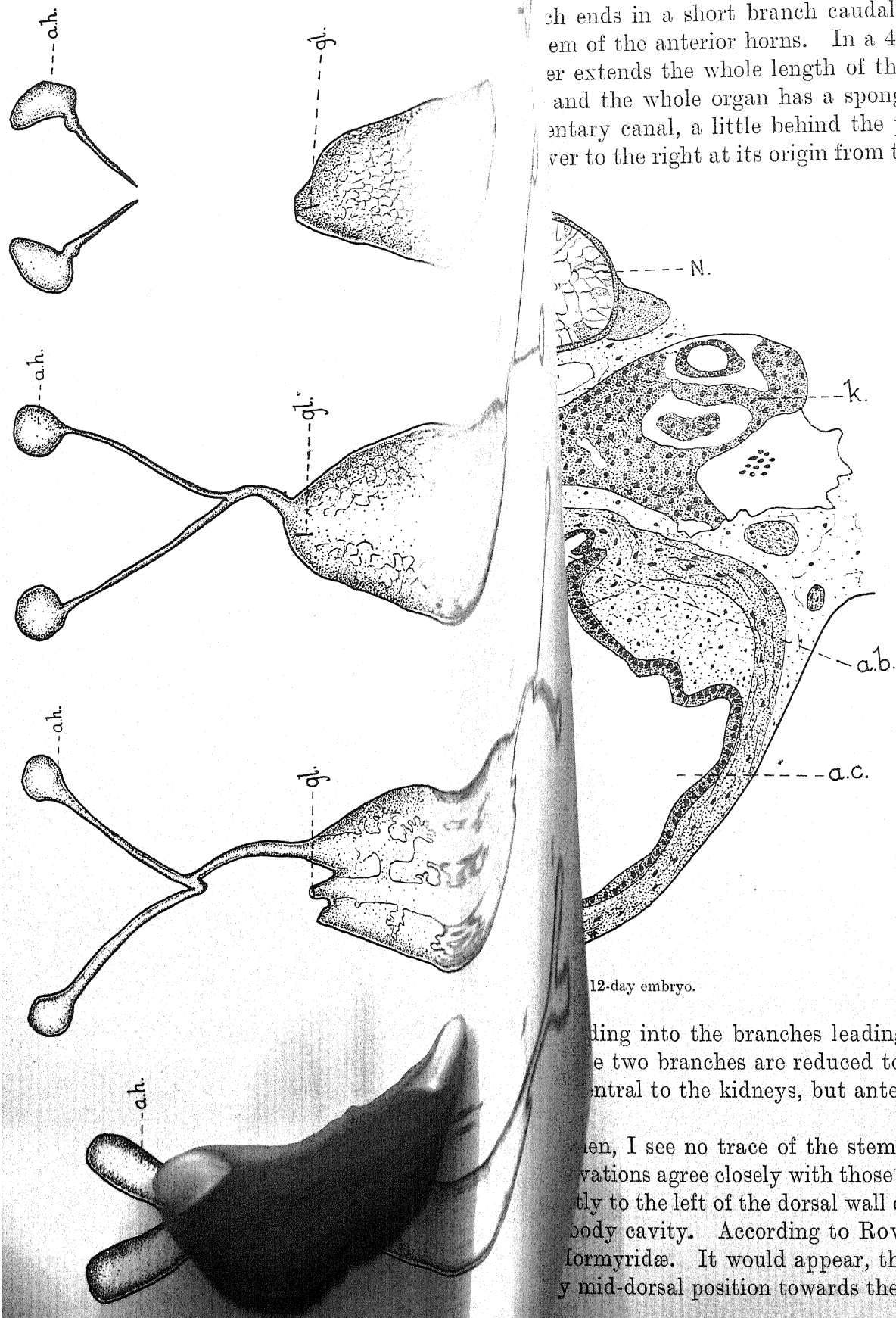


FIG. 12.—C, in 10-day embryo.

## ON AIR-BLADDER AND LUNGS:

ladder down the middle. Near the anterior end each ends in a short branch caudally and a much longer branch anteriorly. In a 40 mm. embryo the air-bladder extends the whole length of the body cavity, and the whole organ has a spongy appearance. The pulmonary canal, a little behind the pharynx. The air-bladder is derived from the air-bladder,



12-day embryo.

...ing into the branches leading to the vesicles. The two branches are reduced to narrow, almost central to the kidneys, but anteriorly they bend

...en, I see no trace of the stems of the vesicles, observations agree closely with those of ASSHETON (2). ...ly to the left of the dorsal wall of the alimentary body cavity. According to ROWNTREE (35), the formyridæ. It would appear, therefore, that the y mid-dorsal position towards the left.



ERLD (11) describes a roomy vacuity in the side wall of the skull of *Gymnarchus*, in close relation to the otocyst and covered over by a thin, oval, shell-like bone. The presence of this thin bone may be the explanation of the loss of the air-bladder connection of the vesicles, since it will physiologically serve the purpose of a tympanic membrane. This same cavity in the skull is described by RIDWOOD (33), and TATE REGAN (31) states that there is in the *Mormyridæ* "on each side of the skull, superiorly, a lateral foramen lodging a vesicle which has lost its connection with the air-bladder." BUDGETT, in his diary of the expedition to Uganda, states that the sacs of the anterior horns of the air-bladder are blown out tight; that there is a stem with a hollow canal in the skull bone, but no apparent opening into the air-bladder.

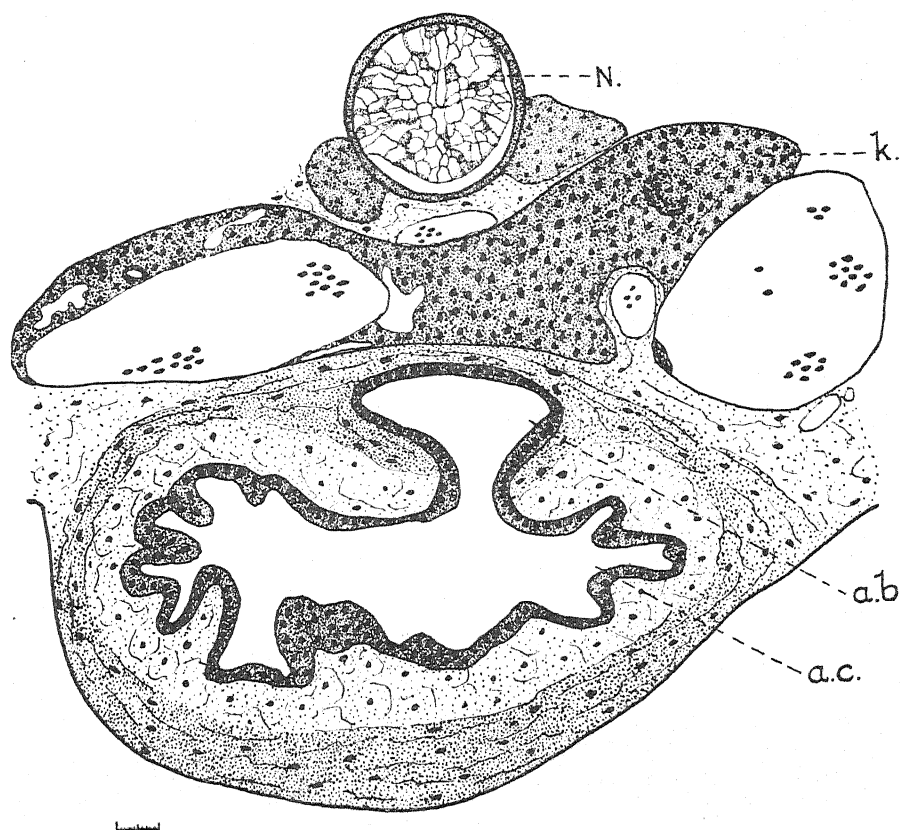


FIG. 12.—E, in 43-day embryo.

He also states that this bulbous horn derived from the air-bladder is present in all the *Mormyridæ* which he has dissected.

In the specimen which I have dissected, there are present at the sides of the skull the two vesicles in close contact with the otocysts. Each has a short duct running caudally and towards the middle line, in the bone of the floor of the skull. These ducts end blindly just before they meet, and there is no trace of the connecting tube which at earlier stages united them to the anterior end of the air-bladder (fig. 14).

It would appear, therefore, that in *Gymnarchus* the connection between the otocyst and the air-bladder is degenerating, though the air-bladder itself is to some extent a respiratory organ.

One point of interest in the development of the air-bladder in *Gymnarchus* is that, though when the rudiment first appears, the œsophagus is an open tube (fig. 12, A-B), at a later stage the walls of the alimentary canal are approximated so as to give the appearance

# ANTYNE ON AIR-BLADDER AND LUNGS :

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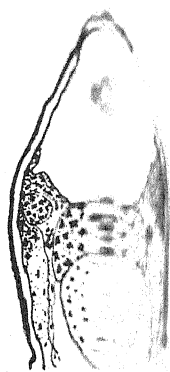
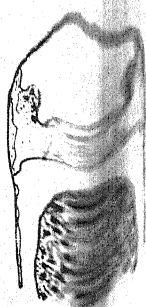


FIG. 1.



a still further reduction function, with the accompaniment of

The evolutionary stage and paired lungs with reduction of the left and completed in the adult possibly due in large measure to

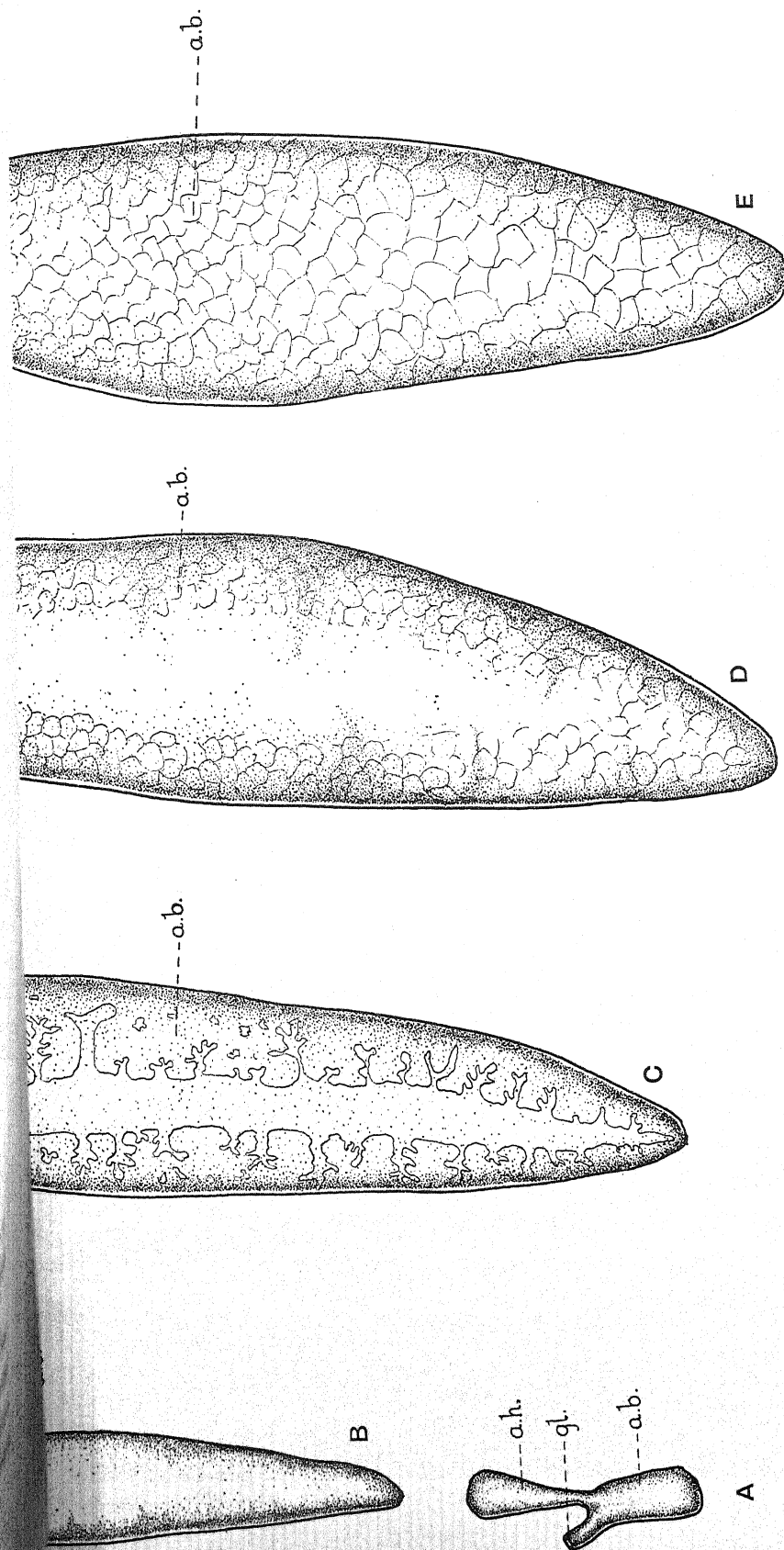


FIG. 13.—Drawings of different stages in the development of the lung of *Gymnarchus*. A, from 5 mm. embryo. B, from 18 mm. embryo. C, from 34 mm. embryo. D, from 40 mm. embryo. E, from adult. Earlier stages more highly magnified than later stages.

of a solid rod of cells (fig. 12, C), although the cavity of the groove-like pneumatic duct remains open. I think that this may be the case with *Lepidosteus*, for in the 11 and 10 mm. embryos which I have examined, the anterior part of the air-bladder rudiment is a groove in the dorsal wall of the solid œsophagus. In MAKUSCHOK's Fig. 6 there is a distinct groove in the dorsal wall of the œsophagus, which looks remarkably like the air-bladder rudiment, though he says that it makes its appearance first in an embryo considerably older than the specimen represented in this figure.

#### CALLICHTHYS.

BRIDGE and HADDON (7) describe a widespread degeneracy of the air-bladder and the Weberian apparatus among the Siluridæ; and BRIDGE, in the *Cambridge Natural History* (5), states that the air-bladder is dumb-bell shaped in *Callichthys*, though SAGEMEHL (36) and others say that in some Siluridæ, including *Callichthys*, there is no air-bladder. In embryos of 10½ and 12 mm. of this fish (fig. 15, A-B), there is a large sac on either side of the head extending from the otocyst to a little distance beyond the gill clefts. In both specimens the two cavities, near their posterior end, are in communication with one another by a narrow duct lying ventral to the notochord and the aorta, but dorsal to the kidneys and alimentary canal. There are traces which indicate that there is a connection between this duct and the alimentary canal at earlier stages of development. These vesicles may, I think, be taken to be part of an air-bladder, which has degenerated except for the anterior horns.

#### EVOLUTIONARY HISTORY OF THE AIR-BLADDER.

The observations chronicled in this paper enable us to picture more fully the probable evolutionary history of the transition from the bilaterally symmetrical, ventrally placed, paired lungs to the dorsal and unpaired

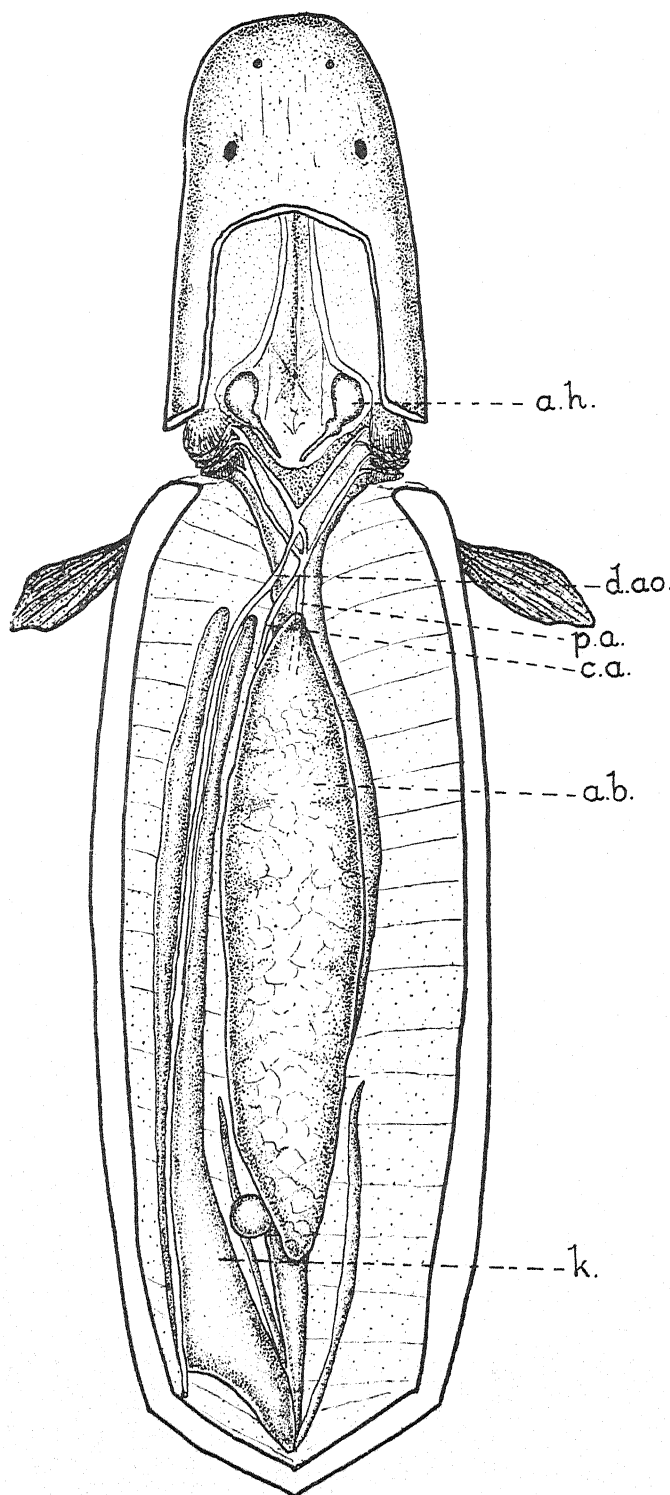


FIG. 14.—Dissection of adult *Gymnarchus*; kidneys displaced to the left to expose the air-bladder.



air-bladder of the modern fish. TRACY (39) has worked out the probable later stages of evolution from the simple air-bladder of *Salmo*, with its anteriorly placed pneumatic duct, to the complex organ present in Physoclistic fishes. The transition from the air-bladder as it is in such forms as *Amia*, to the condition shown by the air-bladder of *Salmo* is primarily

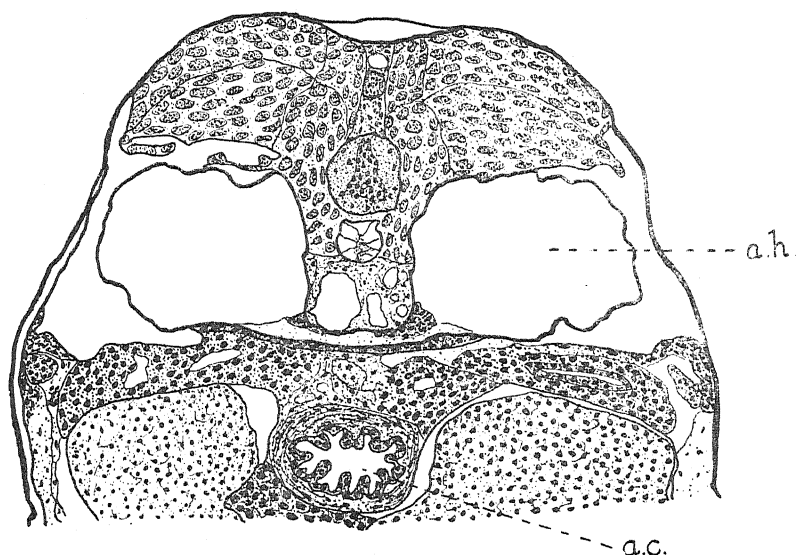


FIG. 15.—Sections through air-bladder of *Callichthys*. A, in 10½ mm. embryo.

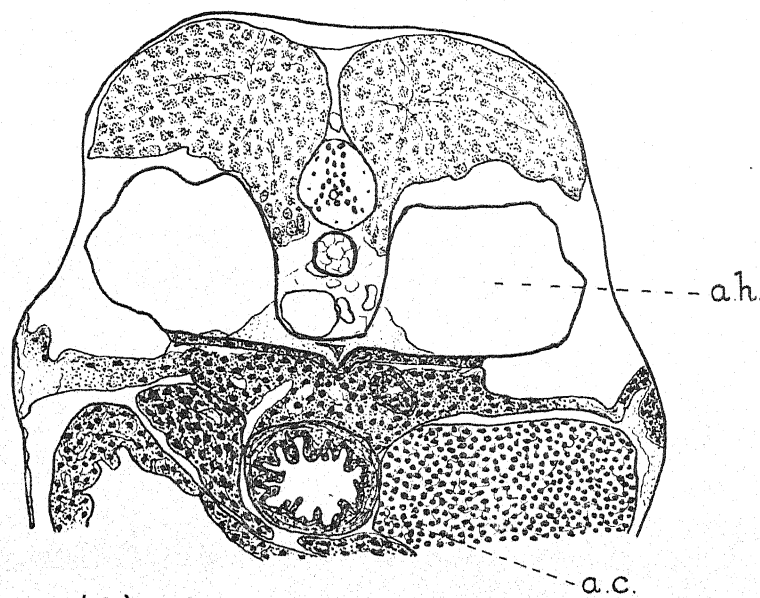


FIG. 15.—B, in 12 mm. embryo.

a still further reduction of the respiratory, and a fuller development of the hydrostatic function, with the accompanying changes in the form and blood supply of the organ.

The evolutionary stages, as far as they can be traced, seem to be : first, normal, ventral, and paired lungs with the usual pulmonary blood and nerve supply ; secondly, the gradual reduction of the left and enlargement of the right lung, seen in its early stages in *Polypterus* and completed in the adult *Ceratodus*. This predominance of the right over the left lung is possibly due in large measure to the position of the stomach well down to the left side.

The next stage is illustrated by *Amia* with its "pulmonoid" air-bladder, which has the normal pulmonary nerve and blood supply, but opens dorsally into the alimentary canal. *Lepidosteus*, again, has a pulmonoid air-bladder with pulmonary nerves, but blood coming from the aorta. In *Acipenser* the reduction of the respiratory function is complete and the air-bladder is a simple membranous sac with its blood supply from the dorsal aorta. In *Salmo* the hydrostatic function has developed further and the air-bladder has now "red-glands" in its anterior walls, but it is still a simple sac opening dorsally into the alimentary canal.

*Ceratodus*, *Amia*, and *Lepidosteus*, in their development, show transitory traces of the existence at one time of a left lung; and the change in position of the glottis from the ventral to the dorsal side may be reasonably interpreted as, at least partially, due to the rotation of the alimentary canal round by the right, as has already been shown by the work of MOSER (26, 27), KERR (20), and others.

I should like to take this opportunity of expressing my gratitude to Professor GRAHAM KERR for his unfailing interest and his invaluable help and advice in the course of the research recorded in this paper. I would also thank the Senate of the University for awarding me the Strang Steel Scholarship to enable me to carry on my work in Glasgow. I am further indebted to the Trustees of the British Museum for their kindness in giving me one of their duplicate specimens of *Gymnarchus niloticus*.

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XVII.—The Geology of Gigha. By W. J. McCallien, B.Sc., Assistant in Geology, Glasgow University. Communicated by Dr G. W. TYRRELL. (With One Plate and Ten Text-figures.)

(MS. received December 6, 1926. Read January 24, 1927. Issued separately July 14, 1927.)

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1. POSITION AND SURFACE FEATURES OF THE ISLAND.

Gigha is a little-visited island off the western coast of Kintyre and between the latter and the island of Islay. It lies about  $5\frac{1}{4}$  miles south-west of West Loch Tarbert, and a little over  $1\frac{1}{2}$  miles from the nearest point of Kintyre where the mainland runs out for  $1\frac{1}{4}$  miles in the low, sandy, raised beach of Runahaorine (figs. 1 and 10).

The island is 6 miles in length from north-east to south-west, and has a greatest breadth of 2 miles. All round it are innumerable smaller isles, all elongated in the same direction as Gigha. Of these the most important are Cara, 1 mile from north-east to south-west by  $\frac{1}{2}$  mile in breadth, and Gighalum,  $\frac{1}{2}$  mile by  $\frac{1}{5}$  mile, and Craro, which is smaller still (figs. 2 and 10). The island forming Ardmish Point, on the eastern coast of Gigha, and Eilean Garbh, at the north-eastern end, will be dealt with here as if they were part of the main island, since at low tide they are connected with it by sandy isthmuses.

The highest point in Gigha is near the centre of the island, where the land rises to 331 feet above sea-level at Creag Bhan. One or two other eminences which are conspicuous are

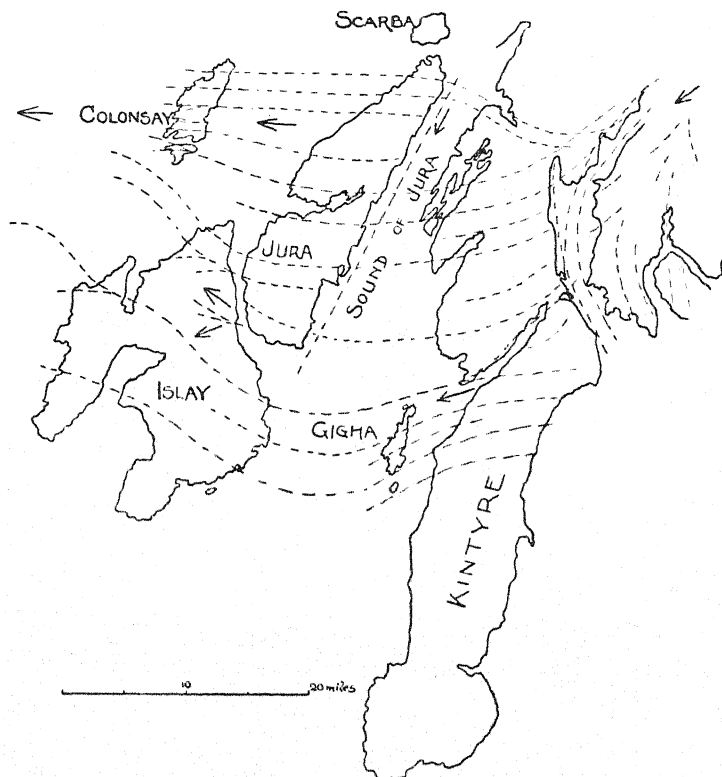


FIG. 1.—Index map showing position of Gigha and direction of ice-movement.

Meall a' Ghلامaidh (260 feet), on the western coast, Cnoc Coille Bharr (225 feet), immediately west of Gigha hotel, Cnoc Largie (219 feet), on the southern side of East Tarbert Bay, and the two peaks of Cnoc nan Gobhar (185 feet) and Carn na Faire (126 feet) on the northern end. Eilean Garbh rises to 157 feet.

As is best seen from the steamer, or from the opposite mainland of Kintyre, Gigha is a long low island of grassy platforms, with three more or less similar hills (Creag Bhan, Cnoc Largie, and Cnoc nan Gobhar). The central part of the island is higher than any other, and immediately on the northern side of this high ground is the lowest part of the island connecting East and West Loch Tarbert.

All around the coast are many long rocky points all running in the same direction as the length of the island, from north-east to south-west (or from east of north to west of south) (Plate I, fig. 1). Behind the lowest raised beach are conspicuous cliffs, and the island is made up of one or two well-defined ridges, separated by valleys filled with raised-beach deposits and running with the grain of the island. The valleys are sometimes occupied by fairly extensive freshwater lochs, the two largest of which, Upper Loch and Mill Loch, in the western part of the island, are of artificial origin. The best example of a very elongated loch between two parallel ridges is Tarr an Tairbh, between An Gortan and Mullach Mor. On the whole, however, the valleys are cultivated, and it is not uncommon to find minor ridges of harder



FIG. 2.—The islands of Cara and Gigha from the north.

"And Cara's isle like giant corse lay near,  
Stretch'd out in state, upon a crystal bier."

rock projecting up through the ploughed fields all along the length of a valley. Only the western portion of Gigha is unsuitable for cultivation.

It is obvious, therefore, that the grain of the island is north-north-east to south-south-west, and the main road runs for about 3 miles in the same direction from the pier on the southern end to Druimyeon More farm, and the greatest height which it reaches in that distance is 64 feet at the post office. From Druimyeon More the road crosses a ridge of hard rock of over 70 feet in height before entering another stretch of flat ground and continuing for about a mile in the same direction as in the first part of its course.

Beautiful sandy bays are abundant around the whole coast except in the central reaches of the western shore-line, and they are remarkably well developed in Grob Bagh to the south, and in Bagh Rudha Ruidh, and Bagh na Doirinne, separating Eilean Garbh from the mainland. Other large sandy bays are found at East and West Tarbert, Druimyeon Bay, and Ardminish Bay.

The western coast is for the most part bold and rocky. It falls in cliffs which are parallel to the strike of steeply dipping schists from heights of over 100 feet down to sea-level (Plate I, fig. 2). The fact that the cliffs so nearly coincide with the dip of very schistose rocks from Meall a' Ghلامaidh to Meall Aird-aillidh (300 yards south-west of the Corn Mill) increases considerably the danger of walking along their summits, for, at intervals along the coast from Cnoc Loisgte southward, small landslides are abundant and large fallen blocks form a platform at sea-level at the base of the cliffs. Besides these vertical walls which the island presents to the Atlantic, the western coast is traversed by great gullies, 20 or 30 feet across,

and running inland at right angles to the cliffs. Some of these gullies contain, either at their base or half-way up, large caves, which continue underground great distances beyond the termination of the external cleft. Examples of such caves are Uamh nan Calaman (north of Meall a' Ghlamaidh), Uamh Mhor (a little further north), and Uamh Cnoc Loisgte. Caves and fissures such as these are found everywhere on the coast of Gigha.

The present shore-line, where rocky, is often extremely difficult to traverse, on account of the fact that differential weathering has removed the softer micaceous schists which are intercalated with quartzose varieties, or with epidiorite; the latter are left projecting as knife-edges. Nor are these continuous for any distance, for as a rule they have been cut across by jointing and by the sea, so that the resulting surface consists of a series of almost vertical, sharply pointed, rods of rock (Plate I, figs. 2 and 3). This is especially the case in the quartzites.

The epidiorites weather with a characteristic honeycombed surface. Massive varieties of these, however, such as those forming Eilean Garbh, Ardminish Point, or Carn Leim, retain their perfectly smooth and glaciated surface, but are broken up into a series of cuboidal blocks.

Dykes are everywhere characteristic features of the shore-line of Gigha, and from the cliffs they project into the sea as high bare walls (Plate I, fig. 5). Many of the large gullies above referred to (between Uamh Mhor and Uamh nan Calaman) are worn out along the edges

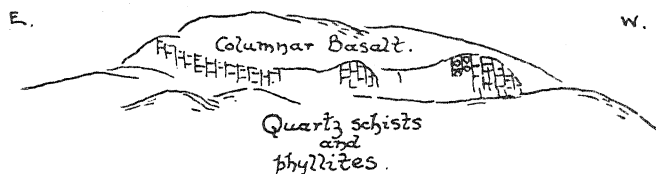


FIG. 3.—View of Cnoc Loisgte from north.

of the dykes. The gully at Uamh Mhor is along a north-west-south-east fault, and is parallel in direction to all the others.

## 2. IMPORTANCE OF THE GEOLOGY OF GIGHA.

The structure of the island of Gigha is important in that it represents a continuation in a south-westerly direction of the geology of South Knapdale. Judging from the map it shows an apparent approach of the South Knapdale rocks to those of Kintyre. In fact, I thought before I visited the island it would show better than the mainland the relations between the Ardrishaig group and the underlying schists. Further, it shows a change in the direction of the strike of the Ardrishaig group from north-east-south-west to east of north-west of south, corresponding to the curving of the schists in Kintyre. From the abundance of epidiorite outcrops on the published map I was looking forward to an interesting study of these rocks, and the relations of the subdivisions of the sedimentary schists appeared attractive, while several outcrops of Green Beds (p) excited suspicion.

Lastly, the size of the island is such that it invited a detailed investigation not only of its structure, from the point of view of South-West Highland tectonics, but also of its igneous rocks, its raised-beach deposits, and the development of its present outline.

I have mapped the whole island on the scale of six inches to the mile.

## 3. PREVIOUS WORK.

No description of this island has been published since MACCULLOCH's *A Description of the Western Islands of Scotland*, 1819, but, since our knowledge of the rocks and structures



of South-Western Scotland has been greatly increased within recent years, it will be possible to pass over many of MACCULLOCH's remarks.

His general description of the rocks, however, is sufficiently interesting to merit quotation here. Thus he states (ii, p. 279):—

“From the frequent alternations that here take place among the different rocks, it is impossible to assign the lowest place to any. This indeed is the general character of the whole series wherever it occurs. It may only be remarked, that quartz rock alternating with micaceous schist prevails on the eastern quarter, and chlorite schist on the western; and that, as far as the island alone is concerned, the former is therefore the lowest, and the latter the uppermost in place. But in the intermediate space, these three rocks are also found alternating, with the further addition of various hornblende schists; the quartz rock, however, in a very minute degree only, the chlorite schists in extensive beds. This latter rock indeed, under various modifications, seems to form the principal part of the island; hornblende schist under different aspects constituting the chief part of the remainder. In a manner equally general it may be remarked, that the hornblende rocks are inferior in position to the chloritic, and they follow the micaceous schist and quartz rock: but they are also found alternating with the former, and even constituting with them several ambiguous and unnamed mixtures.”

In the section devoted to the “General Comparison of the Schistose Isles” (ii, p. 282), he makes many remarks upon the hornblende and chlorite rocks.

The Geological Survey one-inch map of the island, which is included in sheet 20, was published in 1896, but there is no accompanying Memoir. E. B. BAILEY in the maps illustrating his *The Structure of the South-West Highlands of Scotland*,\* includes the island in the Erins Quartzite of South Knapdale and thereby gives a brief statement of the nature of the rocks of the island.

#### 4. SUMMARY OF GEOLOGY.

In the following tabular summary of the geology of Gigha the order of arrangement does not indicate relative age. The metamorphic rocks of sedimentary origin are arranged from west to east in descending order, which is roughly the structurally-descending order in the field.

##### *Alluvial Deposits.*

Blown sand.

Marine alluvium:—

Raised Beaches	{	Lower or “25-foot” beach.
		Intermediate or “50-foot” beach.
		Higher or “100-foot” beach.

##### *Glacial.*

Striæ; and boulders from boulder clay, the latter having been almost entirely removed.

##### *Metamorphic Rocks.*

###### *Northern End of Gigha.*

Carn na Faire Quartzite and Phyllites.  
Port Mor Phyllites.  
Rudh'a' Chairn Bhain Quartzite.

###### *Southern End.*

Meall a' Ghlamaidh Schists.  
Eun Eilean Phyllites.  
Grob Bagh Quartzite and Phyllites.  
Rudha Biorach Phyllites.  
Newhouse Quartzite.  
Ardminish Quartzite.

\* *Q.J.G.S.*, lxxviii, pt. 2.

*Igneous Rocks.*

Non-foliated (Kainozoic): (a) Dykes and (b) One boss.

Foliated: Epidiorite, hornblende schists, and chlorite schists.

Of all these rocks, the epidiorites and raised-beach deposits constitute by far the greatest part of the island. The siliceous and micaceous schists are best developed on the eastern coast, and raised beaches are abundant on the eastern and southern parts. Kainozoic dykes are exceptionally abundant, and there are many that are not indicated on the published one-inch map.

## 5. RAISED BEACHES.

Sufficient has been said already to show that the three beaches common on the west coast of Scotland cover the greater part of Gigha. That is, the 25-foot, 50-foot, and 100-foot raised beaches are found practically everywhere on the island.

The 25-foot is separated from the 50-foot beach by rocky cliffs along the eastern coast. In Grob Bagh, just below the farm of Leim, we find the best terrace of 50-foot beach gravel running right round the bay behind the 25-foot beach and concentric with the present shoreline. Perhaps the largest area of 50-foot raised beach on the island is the grass-covered shingle field between Tarbert and Kinerarach. The 100-foot beach is best developed on the southern half of the island, but small terraces are found to the north.

## 6. GLACIAL GEOLOGY.

On the whole this study is of secondary importance, since the island is so low that at the time when the higher parts of the mainland opposite were covered with glaciers Gigha was covered with floating ice. The signs of the action of the land ice, however, are everywhere abundant, and consist of beautiful *roches moutonnées* and good striae. The top of Creag Bhan, the highest hill on Gigha, furnishes the best examples of both, and these indicate a direction for the ice-movement from north of east to south of west, similar to that of the ice on the mainland (fig. 1).

Boulder clay, except for a few tiny patches, is typically absent, but there are numerous ice-carried boulders in the lower ground, as around, and to the west of, the village of Ardminish.

## 7. METAMORPHIC ROCKS.

(a) *Summary.*

The metamorphic rocks of Gigha, excluding the epidiorites, occupy the greater part of the eastern coast, but small outcrops in the nature of infolds occur at many other parts. These latter, however, are of secondary importance, from the point of view of the composition of the rocks, and examples of almost all the sedimentary schists can be found on the shores of Druimyeon and Ardminish Bays. They consist chiefly of quartzites, quartzite-schists, quartz-mica schists, mica schists, and phyllites, and though on the whole these are so arranged as to be undifferentiable, general subdivisions into quartzites and phyllites have been made. Small gritty and calcareous bands have been met with, but there are no limestones which can be indicated on the map. Local reports, however, state that limestone for burning purposes was once worked in the field opposite Ardminish, but there is no reason for believing that this is correct. A lime-kiln is situated on the raised beach at Port Ban, a short distance north of the pier, and it seems to me that it was placed at this locality because it would be convenient

for the burning of limestone brought by boat from the opposite coast of Kintyre, where good limestone is so abundant and easily obtained.

The details of these schists are given in the following sections (b1) and (b2).

(b1) *Northern End.*

*Carn na Faire Quartzite and Phyllites.*—On the one-inch published map a band of “p” (Green Beds) is mapped at the extreme northern end of Gigha, and its being so named and coloured is most misleading. It is indicated as running steadily in a direction west of south from the coast at this position opposite or south-east of Sgeir Fhiacail, but the outcrop of this band advances sharply eastward in folds and passes within a few feet of the cairn. The rocks here consist of massive epidiorite to the east, and quartzite, quartzite-schists, and phyllites, contorted and squeezed against them. It is extremely difficult to recognise the foliation in the epidiorite, and it is possible that in places the latter may cut across the foliation of the sedimentary schists, as quartzite immediately in contact with the epidiorite does out in both directions. The close resemblance between the schists of different kinds, however, makes it impossible to follow any one particular band. The quartzites and quartzite-schists are very well jointed, and are broken up into a great series of little rhombs.

West of this band, in which quartzite is the predominating rock, comes another of epidiorite, followed to the west in Bagh Beag by phyllites and fine-grained quartzites, with thin seams of  $\frac{1}{2}$  inch or so of limestone, in which cleavage masses of calcite are abundant. This occurs about 580 yards north of An Doirlinn, separating Eilean Garbh from the mainland.

*Port Mor Phyllites.*—This is a more or less well-defined horizon which is easily studied in shore sections, although inland it is entirely covered with raised-beach material and a vegetation of grass, moss, and heather.

The northern shore section stretches from Rudha Bhuidhe (including the point itself), to Traigh nan Beachan, and the boundaries run in a general south-south-west direction till they meet the coast again in the northern shore of East Tarbert Bay.

In a small bay worn out along the strike of the rocks between Cnoc nan Sgularan and Port a' Gharaidh Dubh the phyllites are extremely rich in iron pyrites, sometimes scattered as well-defined crystals through them, but in one band quite massive, making a seam of from 1 inch to  $1\frac{1}{2}$  inches wide. The phyllites on either side of this seam are coloured a bright green with malachite.

In this locality quartzites also occur, and are finely foliated, with surfaces covered with white silvery mica. They are seldom gritty, but occasionally contain brownish lenticles of felspar and grains of blue quartz.

Greenish chloritic phyllites are difficult to distinguish from sheared epidiorites.

Small thrust-like lines of junction are found between the phyllites and quartzites west of Port a' Gharaidh Dubh. In bands of epidiorites which occur on the shore at this place, lenticular infolds of sedimentary schists and massive quartzite are often found. On the shore opposite Eilean Niall, which is separated from the mainland by a north-east-south-west quartz vein, the phyllites are rich in biotite and good strain slip cleavage is developed.

*Rudh'a' Chairn Bhain Quartzites.*—These follow to the east the phyllites of the last group and form the whole section on the eastern point of this part of the island. Their exact boundary with the phyllites to the east is difficult to fix, on account of the fact that they are intimately folded with one another, and the rocks at the boundary are intermediate in composition. The last group was defined as a group of phyllites, but quartzites were also met with in it, though subordinate in amount to the phyllites. In the present group phyllites, too, are



found, but quartzite is the most important rock. In the bay on the northern side of Rudh'a' Chairn Bhain the boundary between the two groups has been inserted in Traigh nan Beachan, the small bay just west of Rudha Port an Tigh.

(b2) *Centre and Southern End.*

*Meall a' Ghلامaidh Schists.*—This is rather an ill-defined infold of quartzites, phyllites, and micaceous schists, in epidiorite. It forms the summit of Meall a' Ghلامaidh and the shore section from Sloc na Stuire to Uamh Mhor. Here it meets a north-west to south-east fault, which displaces the sedimentary schists on the northern side to the south-east, and brings the main mass into contact with epidiorite containing subordinate amounts of siliceous and micaceous schists.

South-east of Meall a' Ghلامaidh there are several infolds of white, massive, fine-grained quartzite, and in the cliff section west of Druim Meadhonach of phyllites and quartz-mica schists.

*Eun Eilean Phyllites.*—The whole south-western extremity of Gigha is coloured as epidiorite on the published one-inch map, but there are many localities where sedimentary schists are abundant. For example, quartzites from the last group outcrop on the shore at the western head of Portan Craro. Another small exposure of siliceous schists and phyllites on the shore, and in a burn section in Port an t-Samhlaidh, south-west of Ardlamey, leads me to believe that most of these elongated valleys, now covered with raised-beach alluvium, have been cut out along such schists, while the ridges on either side are of epidiorite.

The Eun Eilean outcrop stretches from Lag nam Feusgan to the shore in Poll Mor, and the eastern half of Eun Eilean is composed of micaceous and siliceous schists.

*Grob Bagh Schists.*—As stated above, no indication of sedimentary schists appears on the published map from Leim westward and northward along the coast, until we come to the Meall a' Ghلامaidh phyllites. The present group is another example of a series of schists more or less covered with alluvium. The Grob Bagh series begins at Rudha Bhuidhe with massive pure white quartzite intersected by quartz veins, and is interrupted once or twice by epidiorite sills; but it forms the whole bay right across to the massive epidiorite on the shore north-west of Carraig an Sgonnian. After the massive quartzites above referred to, we get a thick band of phyllites, and then alternations of micaceous and quartzitic schists with quartzite (fig. 4).

*Rudha Biorach Phyllites.*—On the one-inch map the boundary between the Carn Leim epidiorite of the extreme southern point of the island, and the quartzite to the east, is drawn

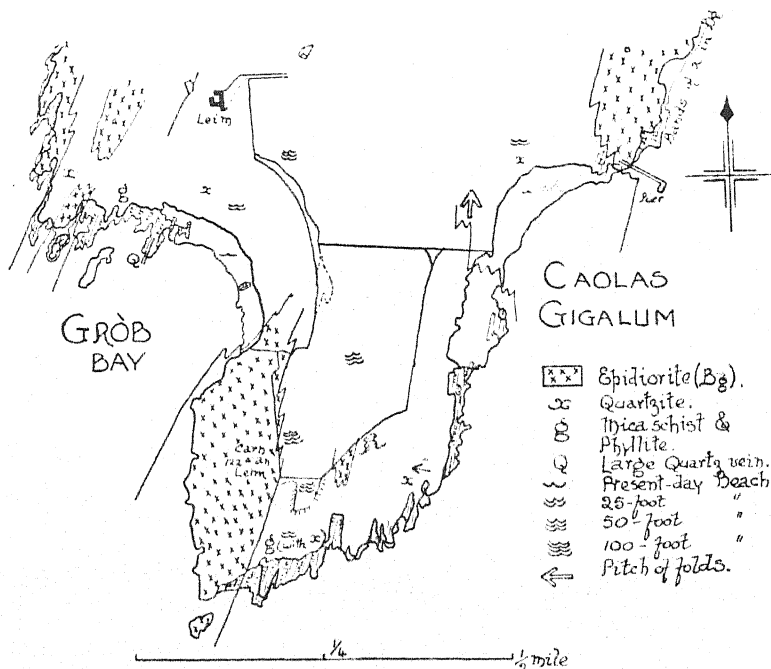


FIG. 4.—Sketch map of Southern Gigha.

somewhere about Port Beulan Faing, or Uamh Mhor, but the true boundary is a considerable distance to the west. The massive epidiorite of Carn Leim occurs on the small island Eilean Leim, but does not stretch across the first small bay to the east of it. That is, the boundary between these epidiorites and the present group is on the western shore of Port Mor. East of the epidiorites we get a series of quartzites, schists, and phyllites, probably a continuation of the Grob Bagh group, interrupted by the intrusion of the Carn Leim igneous rock.

*Newhouse Quartzite.*—This is a continuation to the east of the above group, and probably a direct continuation of the Rudh'a' Chairn Bhain quartzite. It meets the shore on the southern side of East Tarbert Bay at Eilean na Caorach and Port nan Corrain to Bagh Rudh' an Stearnail. South of this, however, it is lost in the raised-beach deposits, which occupy the tract of country traversed by the main road from Druimyeon More to Newhouse. Once or twice in that distance, bands of quartzite outcrop through the shingle, as *e.g.* at the roadside a little past the manse, and east of the village of Ardminish. The shore section on the extreme south of the island is interesting and the rocks can be studied in the shore sections or in the cliffs behind the 25-foot raised beach. In the cliffs immediately behind Port Beulan Faing is an outcrop of epidiorite, which does not occur on the shore, and instances of a similar type of difficulty have been met with in other parts of the island. At Eilean a' Bhran-phuirt, and on the shore to the north-west of it, the siliceous schists advance their outcrop to the east in a series of folds pitching steeply northward or north-eastward. The folding and pitch are

admirably seen here where siliceous schists are found reaching the surface from beneath massive quartzites, and at right angles to the normal direction of strike. Likewise, at the pier, the boundary between the quartzites and epidiorites runs in an east of south direction.

*Ardminish Bay Quartzite.*—This includes all the siliceous and micaceous rocks from Rudh' an Stearnail (south-east of East Tarbert Bay) across to Rudha Breac and the western shore of Druimyeon Bay. The outcrop here shifts somewhat eastward, and rocks belonging to this group (with epidiorites) form Ardminish Point and cross to Ardminish Bay. On the northern shore of this bay most of the rocks enter the sea and reappear again to the south, east, and west, of Eilean a' Chuil, where they are divided into two by a broad band of epidiorite, which in all probability is a continuation of that in Ardminish Point. Eilean a' Chuil and Eilean Brachach are both fashioned out

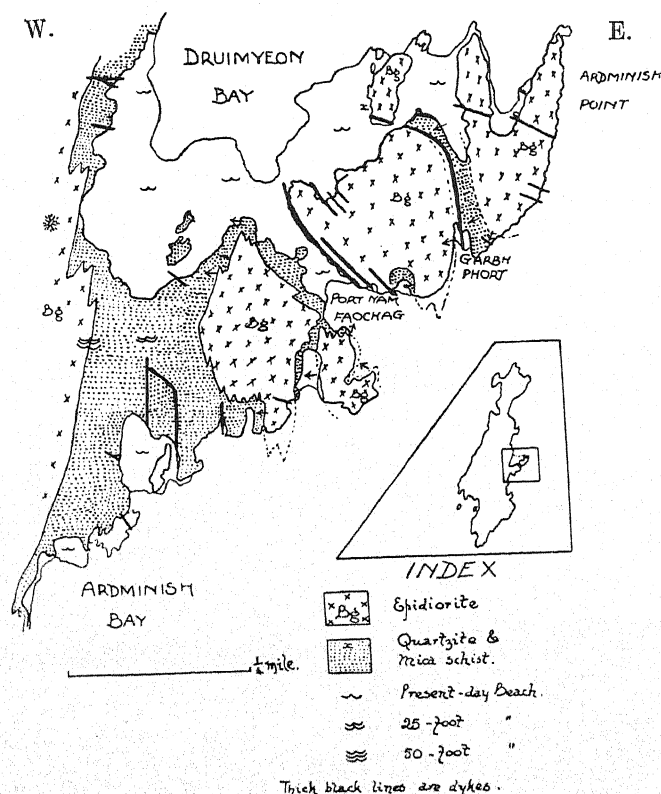


FIG. 5.—Sketch map of Ardminish Point showing infold nature of the epidiorites.

of the epidiorite, which begins a few yards to the west of the latter island. Both of the islands of Cara and Gighalum are composed of quartzites and epidiorites of this group.

The western boundary actually lies a few yards further west than is indicated on the one-inch map.

This group consists of massive quartzite, quartz-mica schists, and soft silvery phyllitic mica schists. On the western shore of the small bay at An Sailean (Druimyeon Bay) are lenticular bands of extremely coarse grits, which weather with the characteristic rough surface of gritty rocks, where the grains project upwards above the matrix. The latter, in this case, is very calcareous, and effervesces freely with cold acid. The pebbles are of clear pale blue quartz, and are not granulitised. The rock is separated into layers, at intervals of about  $\frac{1}{10}$  inch, with silvery muscovite, and some bands are rich in secondary biotite. The small flakes of black mica are sometimes scattered irregularly through the rock. These bands of grit are interesting, as they are the only rocks of that nature found on the island.

On Rudh' an Stearnail, between East Tarbert Bay and Druimyeon Bay, the soft silvery phyllites, interfolded with massive quartzites, are laden with bands extremely rich in secondary biotites. These latter often project from the weathered surface of the phyllites in crystal rods and with this arrangement they resemble hornblende needles. Application of a pin-point, however, reveals the perfect cleavage of mica, and the rods fall to pieces. The secondary micas are developed in well-defined bands, and are especially prominent along strain slip cleavages. The outlines of some of the folds are accentuated by the concentration of biotite around them (fig. 9c).

Along, or closely associated with, some crush breccias on the shore below the manse is a band of dense black mica schist, which may mark the position of a small thrust.

## 8. IGNEOUS ROCKS.

### (a) *Non-foliated. Kainozoic.*

The northern end of Jura, and Knapdale, from Loch Crinan to West Loch Tarbert, contain very few Kainozoic intrusions in the nature of north-west dykes. The area to the north-east of this belt, stretching as far south-east as the Glasgow district, and the country to the south-west, from southern Jura and Gigha across into Kintyre and Arran, are extremely rich in such dykes. The dykes in these two areas belong respectively to the Mull and Arran Swarms of the Geological Survey.\* The present island has furnished an interesting study of the field relations of these intrusions. As already stated, the dykes often stand up through the softer schists as large vertical walls (fig. 3 and Plate I, fig. 5), while at other times they have yielded to the agents of denudation more easily than the schists, and are now represented by gullies.

These dykes run essentially in a north-west to south-east direction, but a glance at one or two of the text-figures here will show that, oftener than not, their course is extremely irregular. Take for example the large dyke on the northern shore of West Tarbert Bay

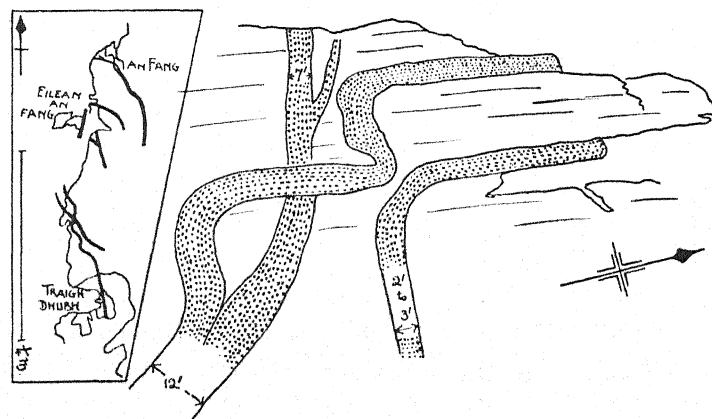


FIG. 6.—Rough sketch map of dykes on shore, An Fang, north of W. Tarbert Bay. Inset is coast from An Fang to Traig Dhubh (thick black lines are dykes).

(fig. 6). Inland at An Fang this is apparently one dyke with a width of 12 feet. On the shore, however, it splits into two branches of 6 feet each; one of these crosses the other as

\* *Mem. Geol. Surv. Scotland*, "Tertiary and Post-Tertiary Geology of Mull, Loch Aline, and Oban," 1924; map, p. 357.  
TRANS. ROY. SOC. EDIN., VOL. LV, PART II (NO. 17).



illustrated, and the latter again splits into two near sea-level. A short distance south of this between Port na Cleire and Traigh Dhubh a north-west dyke cuts a north and south part of another dyke. That the direction of these dykes is connected with, and controlled by, the jointing of the schists is illustrated by a 4-foot dyke in Port Allaidh, north-west of Meall a' Ghlamaidh. In the short distance between the raised beach and the sea this dyke has about five sections running at right angles to the strike of the schists, and as many parts run along the strike. Perhaps an even better example is the small dyke at Leac Bhuidhe, north-west of Creag Bhan. As seen from the cliffs above, the shore here seems to be cut by a dyke of uniform width. But, on closer examination, it is found that the dyke does not continue to the sea in a uniform manner, for it divides into two branches, which occupy only the margins of the joint block.

East of Druimyeon More, on the shore, is an 18-foot dyke, which is displaced its own width north-eastward along the strike of the schists, but a thin dyke connects the two main masses. A dyke with good rectangular banding is seen on the raised beach east of Achamhinish in Ardminish Bay; and in the one-inch map a semicircular dyke, which I have not seen, is mapped on Ardminish Point. The dykes that I have mapped on this point are shown in fig. 5. The Port an Sgiathain dyke shows three right-angle bends in a very short distance.

At An Sailean an unmapped dyke follows a fault with 30 feet of crush breccia, running in a direction north of west to south of east. On the shore to the south there is a small intrusion (apparently a sill), 1 foot in thickness, running along the strike of the phyllites and quartzites.

Of about twenty-seven slides of Kainozoic intrusions from the island of Gigha which I have examined, fourteen or half are crinanites and the remainder are olivine-dolerites. Little description need be given of these rocks, as they closely resemble those already described in the *Memoir* on the "Geology of Knapdale, Jura, and North Kintyre" (pp. 115-118).

In hand specimen, the crinanites are fine-grained greyish rocks; but occasionally coarse varieties are met with, and in these analcite can be made out with the naked eye. They usually contain numerous cavities filled with radial zeolites. The dyke parallel with the coast at Creag nan Con contains fairly abundant iron pyrites.

Microscopically they are beautifully ophitic analcite-dolerites with large plates of purple augite containing laths of labradorite, and more or less idiomorphic crystals of olivine broken up and traversed with veins of serpentine. Triangular and irregular spaces between the other minerals are filled with analcite.

The purple augite is often considerably darkened by a separation of minute grains of magnetite, and besides this purple variety there is sometimes a pale green augite which is non-pleochroic. In some rocks the amount of analcite is exceedingly small and perhaps only one triangular space filled with the mineral can be found in a whole slide. In others it is very abundant and makes up almost half the rock. This is the case in the dyke at An Doirlinn, Ardminish Point, and in a dyke west of Sgeir Liath (near Eilean Liath). The analcite usually has a brownish colour, due to turbid decomposition products, and many of the interspaces are filled with a colourless fibrous mineral, probably natrolite. A porphyritic crinanite has been found at Rudha Dubh. This is similar to the others, but contains occasional very large phenocrysts of plagioclase.

The olivine-dolerites contain purple augite, colourless or serpentinised olivine, plagioclase, and magnetite, but are devoid of analcite. Some very coarse ophitic types, which differ from the crinanites only in the absence of analcite, are closely linked with them by the abundance of spherulitic aggregates.

A small boss of coarse crinanite occurs a little south-west of Tarbert farm.

The schists in contact with most of the above intrusions are much altered. They are hardened and darkened in colour, with the separation of much magnetite. Their micas are nearly always changed, and some of the rocks are a network of black and dark brown material and quartz grains. The latter are always cracked and broken, and secondary products have made their way along the cracks.

(b) *Foliated. Epidiorites and Chlorite Schists.*

The igneous rocks which are older than the foliation of the schists range from very sheared varieties in the form of chlorite schists, through hornblende schists, to massive types in which no foliation can be detected. These last are best developed in Eilean Garbh at the north-western end of the island. Here the coarsest rock is made up of large plates of scaly hornblende, from  $1\frac{1}{2}$  to 2 inches in length and 1 inch across, embedded in zoisite. Though the rock is not foliated in the central parts of the intrusion, the smaller hornblendes are arranged in parallel bands. Other massive but finer-grained epidiorites occur along the eastern coast, and are typified by the rock at Carn an Leim at the southern end. This is a dark green hornblende-felspar rock.

The hornblende schists resemble the last, but are very finely foliated, and the feldspars are inconspicuous. The chlorite schists are the very sheared varieties of these types. It is these rocks that have been indicated on the one-inch map as "green schists."

In the epidiorites, and best seen at Leac Bhuidhe, south of West Tarbert Bay, are lenticular cores of green epidotic material with a little calcite, averaging 1 foot by 10 inches in their longest and shortest diameters. The cores are non-foliated, and the foliation of the hornblende schists bends round them (Plate I, fig. 4). Under the microscope, these masses are seen to be composed of yellowish-green epidote and calcite with grains of quartz, a little chlorite, and occasionally crystals of biotite.

The coarse Eilean Garbh rock under the microscope shows large plates of pale green tremolite, and scarcer plates of zoisite surrounded by granular and prismatic zoisite, and muscovite, with quartz, and less frequently felspar, filling interspaces. Sometimes the amount of zoisite increases until the whole rock is composed of phenocrysts of amphibole in zoisite.

The Carn an Leim variety resembles a quartz-diorite and consists of hornblende, plagioclase, and exceptionally abundant iron oxide, with interstitial quartz. There is very little foliation, and the feldspars are often quite fresh, but at other times they are covered with epidote and may be completely replaced by it. In these last cases epidote, quartz, and chlorite become abundant, and there are crystals of biotite.

The best example of a fine-grained hornblende schist was obtained from the north-west of the hotel, and it is composed of hornblende, epidote, and quartz, with subordinate chlorite.

The chlorite schists range from the above to varieties in which the hornblende is not so abundant as the chlorite, and in these calcite reaches large amounts, quartz occurring in minute grains. Biotite also occurs. In some slides there are porphyritic albites as in the albite schists of Kintyre.

## 9. STRUCTURE.

As has already been said, the sedimentary schists are subordinate in amount to the epidiorites, and as the latter are structureless for the most part, it is difficult to interpret the structure of the island.

The rocks forming Gigha belong to the Erins Quartzite, that series of quartzites, grits, and phyllites belonging to the Ardrishaig group, which is developed in South Knapdale. These quartzites on the mainland north-east of Gigha I have shown \* are much more folded than has hitherto been thought, but their general dip is to the north-west under the other members of the Loch Awe Syncline. Likewise, the quartzites and phyllites on Gigha have a general dip to the north-west, but a study of the minor peculiarities of their structure leads me to believe that the structure of the island itself is synclinal with smaller corrugations. Thus, although we find the sedimentary schists on the eastern coast, and the epidiorites to the west, there are infolds of quartzites and phyllites, similar to those from Ardminish, along the western and southern shores, as I pointed out in the description of the schists.

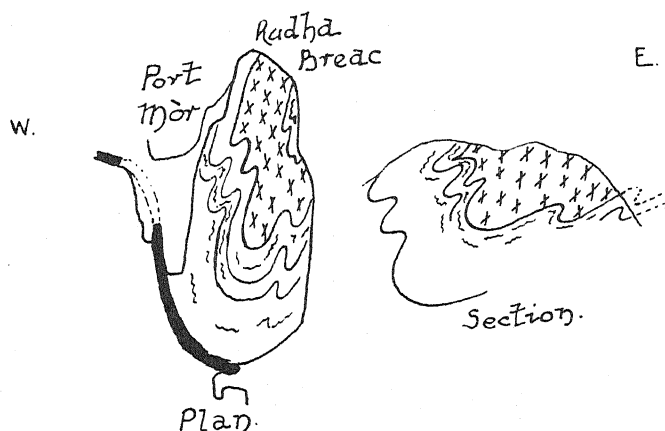


FIG. 7.—Infold of epidiorite on Rudha Breac, Druimyeon Bay.

the diagram illustrating Rudha Breac, Druimyeon Bay, shows a smaller, but none the less interesting, infold of a similar nature (fig. 7).

The quartzites and phyllites themselves are folded with the small-scale isoclinal folding which is so characteristic of the rocks of the Loch Awe Syncline. The type of folding and the nature of the outcrops developed in the massive quartzites are illustrated in figs. 8 and 9.

A section of a large and interesting infold of quartzite in epidiorite is seen on the cliffs at the west of Portan Craro, the little bay north of Craro Island. The small-scale folding here is very complicated.

The pitch of all these folds is to the north-east and can be well seen on Ardminish Point, and in the quartzites and schists west of the pier (fig. 4). Here, as I have said, we find siliceous schists advancing their outcrop to the east and reaching the surface from beneath massive quartzites.

Although it is stated in this paper that the schists of the island belong to the Erins Quartzite, it is impossible to assign any definite horizon of the South Knapdale rocks to those of Gigha.

One fact to me seems certain and that is that the quartzites on Gigha (if they be Erins Quartzite as I believe them to be) belong to the upper part of this group (in the strict stratigraphical sense).

This statement I make because the quartzites are different in character from those in the south-eastern part of South Knapdale, and they resemble the quartzites which are admirably exposed in the Loch Gair section at the entrance to Upper Loch Fyne. It is possible from the development of thick bands of phyllite that the rocks of Gigha might belong to the lower

\* *Trans. Geol. Soc. Glasgow*, xvii, pt. 3, 1925-26, pp. 377-394.



part of the Ardrishaig Phyllite group, but the quartzites are too abundant to make this probable.

Assuming, therefore, that the Gigha schists belong to the upper part of the Erins Quartzite, it is true, as stated in (2) under Importance of the Geology of Gigha, that not only do the rocks here show a change in the direction of their strike, but they show an approach of the South Knapdale rocks to those of Kintyre.

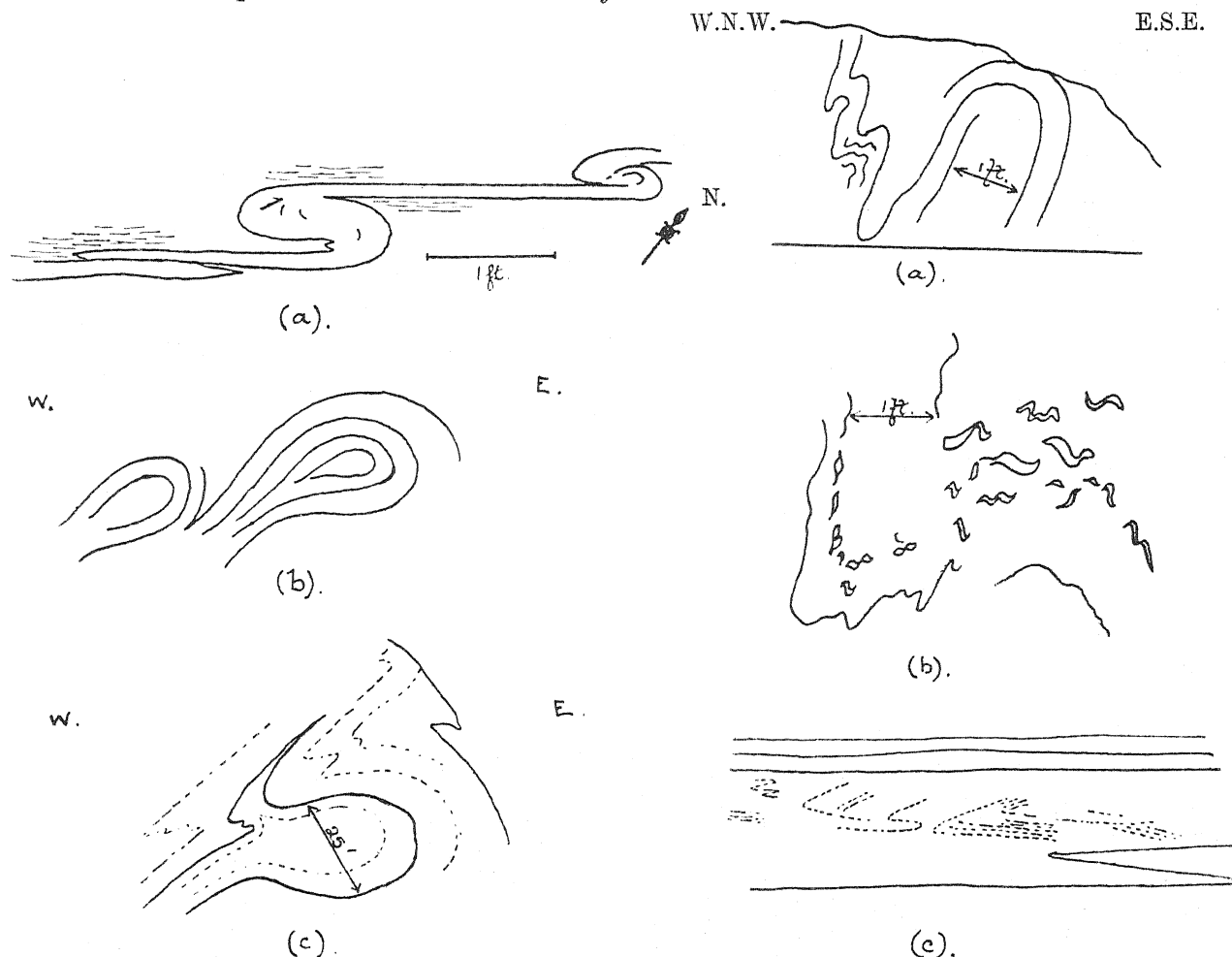


FIG. 8.—Sketches illustrating plan of folds in epidiorite and quartzite. (a) Quartzite, Baraillean Sail shore, Kinerarach; (b) Epidiorite, Sgeir Fhiacail [scale as in (c)]; (c) Epidiorite, Rudh'a' Chairn Bhain.

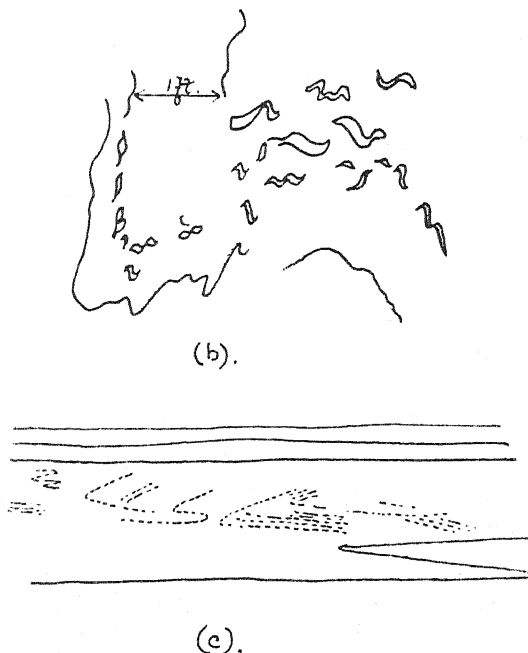
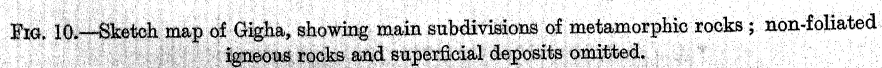


FIG. 9.—Vertical sections of folds in quartzite. (a) Rudha Port an Tigh; (b) Quartz lenticles in quartzite, Rudh'a' Chairn Bhain; (c) Secondary biotites in phyllite band in quartzite, Rudh' an Stearnail.

It seems to me, therefore, that just as the Erins Quartzite is cut off to the north-east by the thrust separating BAILEY'S Loch Awe Nappe from the Iltay Nappe,\* so does it become gradually cut off in the same way to the south-west. Although in a previous paper I stated † I could find very little evidence for a thrust separating the Erins Quartzite from the Stonefield schists in the small portion of South Knapdale where the two are in contact, yet considering the problems of Gigha, South Knapdale, and Cowal as a whole, the approach of the Gigha rocks to the Kintyre (or as it is commonly called, the Cowal) sequence, and the cutting off of the Erins Quartzite to the north-east are best explained by BAILEY'S thrust at the base of the Loch Awe Nappe.

\* *Q.J.G.S.*, lxxviii, pt. 2, 1922, p. 96.

† *Trans. Geol. Soc. Glasgow*, xvii, pt. 2, 1924-25, p. 251.



## 10. ACKNOWLEDGMENT.

The writer wishes to make acknowledgment of a generous grant for personal expenses in Kintyre and Gigha provided by the Government Grant Committee of the Royal Society of London.

## 11. EXPLANATION OF DIAGRAMS.

## (a) GENERAL.

Fig. 1. Index map showing the position of Gigha, and indicating the general direction of ice-movement over the island and in the neighbouring parts of South-West Scotland.

Fig. 2. Sketch showing the characteristic shapes of the islands of Cara and Gighalum.

Fig. 3. Sketch of large basalt dyke intruded into schists and phyllites, and forming Cnoc Loisgte on the western coast of Gigha.

## (b) DETAILED SKETCH MAPS.

Fig. 4. Sketch map of Southern Gigha showing bands of phyllite and quartzite described in this paper, but not indicated on the one-inch Survey map.

Fig. 5. Sketch map of Ardminish Point showing infold nature of the epidiorites in the Ardminish Quartzite. In the mapping of the circular outcrop of epidiorite to the left and in other details this sketch map, also, is different from the one-inch map.

## (c) IGNEOUS GEOLOGY.

Fig. 6. Diagrammatic sketch of dykes on the shore at An Fang, north of West Tarbert Bay. The main dyke to the south-west is here seen to branch into two, and the most westerly of these branches is seen to cut the other. The direction of the branches, too, is determined by the strike of the epidiorites, and by jointing at right angles to the strike.

Inset is a small sketch map of the coast from this to West Tarbert Bay showing the tendency for these dykes to change their course, to branch, and to cut across one another.

## (d) STRUCTURAL.

Fig. 7. Infold of epidiorite in quartzite on Rudha Breac, Druimyeon Bay, showing plan and section of the folding.

Fig. 8. Three diagrams illustrating the curious nature of some of the outcrops of infolded schists:—

(a) Folding in quartzite, Baraillean Sail shore, Kinerarach.

(b) Epidiorite infolds in quartzite, Sgeir Fhiacail.

(c) The same, Rudh'a' Chairn Bhain.

Fig. 9. Three diagrams illustrating vertical sections of the type of folding developed in the quartzites:—

(a) Rudha Port an Tigh.

(b) Rudh'a' Chairn Bhain.

(c) Rudh' an Stearnail, showing development of secondary biotites in quartzites.

Fig. 10. Geological sketch map of Gigha.

## 12. EXPLANATION OF PLATE.

Fig. 1. Druimyeon Bay as seen from the high ground east of Tarbert farm, and showing Ardminish Point, epidiorite ridges, and raised beaches, all running in the same direction, N.N.E.-S.S.W.

Fig. 2. The western coast of Gigha, from the shore west of the Corn Mill to Eilean Garbh. The rocks in the foreground are highly sheared epidiorites.

Fig. 3. Quartzites on the north-eastern coast of Gigha, showing typical weathering.

Fig. 4. Epidiotic spheroids in epidiorite, south of West Tarbert Bay.

Fig. 5. Dolerite dyke, Port an Sgiathain, half a mile south of Ardminish Bay.





Mr W. J. McCALLIEN on "The Geology of Gigha."—PLATE I.

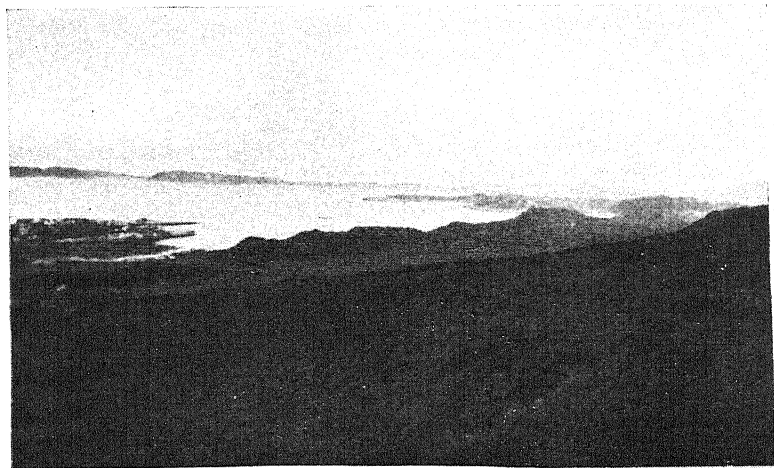


FIG. 1.

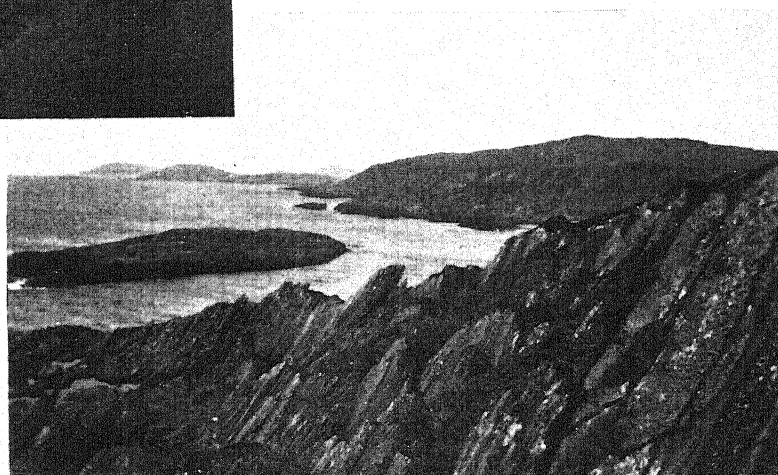


FIG. 2.

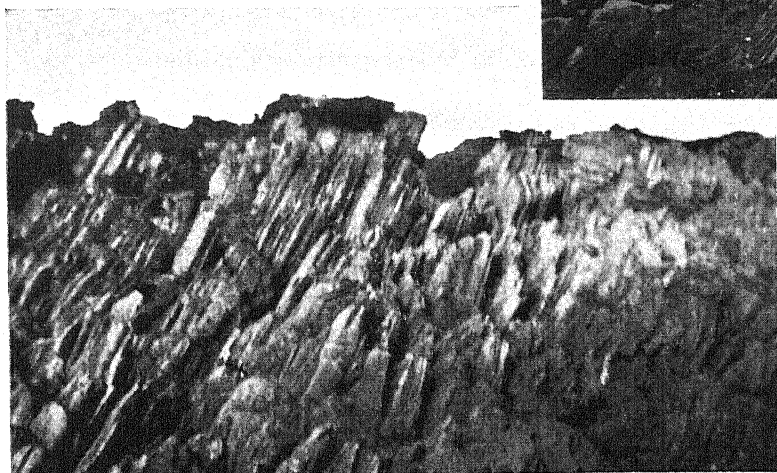


FIG. 3.

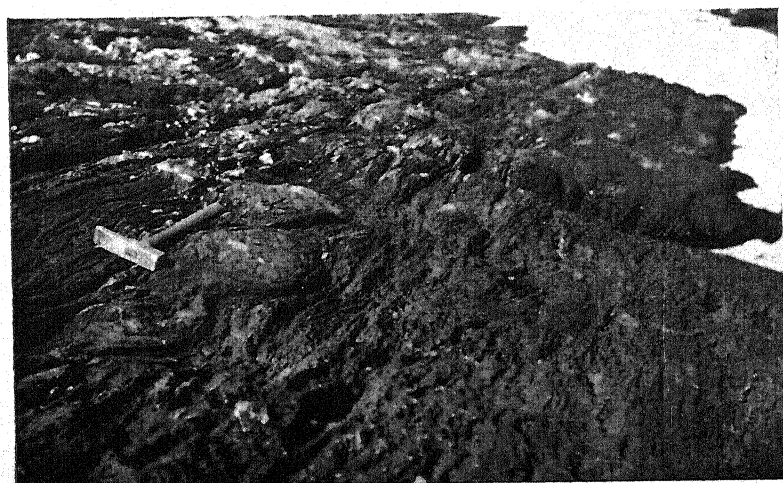


FIG. 4.

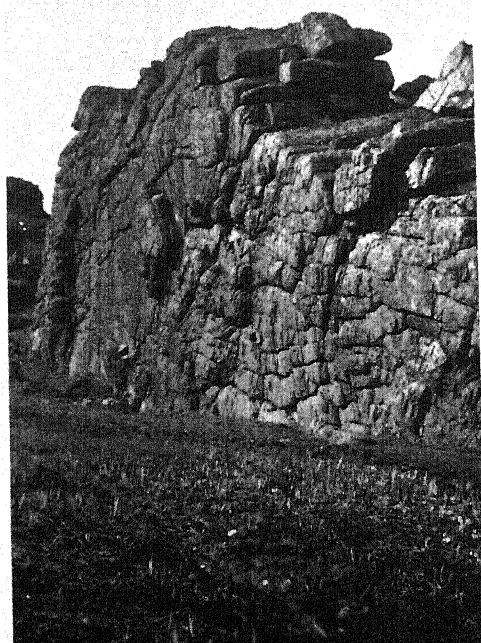


FIG. 5.





XVIII.—Jurassic and Eocene Echinoidea from Somaliland. By Ethel D. Currie, B.Sc., Ph.D., F.G.S., Hunterian Museum, The University, Glasgow. *Communicated by Professor J. W. GREGORY, F.R.S.* (With Seven Text-figures and One Plate.)

(MS. received March 28, 1927. Read June 6, 1927. Issued separately September 24, 1927.)

The collection of echinoids, which is the subject of this report, was made by Mr R. A. FARQUHARSON, M.A., M.Sc., F.G.S., Government Geologist, during his survey of British Somaliland in the year 1923–24. The collection was presented by the Colonial Office to the Geological Department of the British Museum, and the Keeper, Dr F. A. BATHER, F.R.S., has been good enough to allow me to examine and describe these interesting specimens. I have been fortunate in having beside me for comparison the echinoids from Somaliland in the Hunterian Museum, which were collected by Mr B. K. N. WYLLIE, B.Sc., F.G.S., and Dr W. R. SMELLIE, and through them presented by the Anglo-Persian Oil Company. I take this opportunity of expressing my thanks to Professor GREGORY for his interest in the collection and for much kind help.

The collection comprises Jurassic and Eocene species. The Jurassic echinoids are from four localities, as follows :—

#### BIHENDULA.

*Stomechinus* aff. *microcyphus*, Wright.  
*Clypeus wylliei*, Currie.  
*Pygurus smelliei*, Currie.  
*Pygurus* cf. *depressus*, var. *somaliensis*, Currie.  
*Bothriopneustes somaliensis*, (Currie).

#### IDA KABEITAH HILL.

*Acrosalenia* (*Metacrosalenia*) *pseudocidaroides*,  
 Currie.  
*Acrosalenia* (*Metacrosalenia*) *quadrimaliaris*,  
 n. sp.

BIYO DADER TUG OR WELL, GADABURSI,  
 W. SOM.

*Recrosalenia somaliensis*, Currie.  
*Farquharsonia somaliensis*, n. gen. and sp.  
*Echinotiara somaliensis*, n. sp.  
*Holactypus*, sp. indet.  
*Holactypus*, n. sp.

#### DEBERAWEINA, W. SOM.

? *Acrosalenia smelliei*, Currie.  
 ? *Hemicidaritis bihinensis*, Currie.

The above species from Bihendula, with the exception of the *Stomechinus*, were originally described from that locality from the Lower Bihin Limestone. The horizon of the Bihendula echinoid limestone is Bathonian, according to the evidence of the collection of Mr WYLLIE and Dr SMELLIE,\* and the association with these species in the present collection of a specimen closely allied to *Stomechinus microcyphus*, an acknowledged Bathonian species, lends confirmation to this conclusion. The occurrence of *Acrosalenia pseudocidaroides* from Ida Kabeitah, also originally described from Bihendula, shows that the horizon of the Bihendula echinoid limestone is present in the Ida Kabeitah outlier also. Of the specimens from Biyo Dader, Gadabursi, only *Recrosalenia somaliensis* is known, the holotype (Hunt. Mus. E. 764) being from Bihendula. The occurrence of a specimen of this species from Biyo Dader indicates the presence of the same Bathonian horizon in the Western Jurassic series. In confirmation

\* *Monogr. Hunt. Mus.*, vol. i, 1925, p. 2.

simple primaries to all are crowded just before plates being more curved plate complexity (vid.

*Dimensions.*—Diam

*Tumid variety?*

may represent a tumid to be even more curved another. B.M., E. 1— sions: Diameter (D).

*Diagnosis.*—A Metavert series of equal of the two inner series become larger miliaries in irregular

*Material.*—Holotype

*Dimensions.*—Diam

*Locality.*—Ida Kaba

*Description of Holotype*

Edges high, steep, and

*Apical System.*—

4 large, 1 contiguous

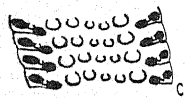
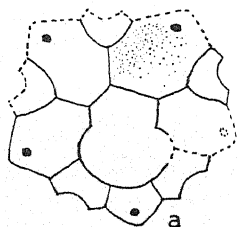


FIG. 2.—*Acrosalenia* (*Metacrosalenia*) n. sp.

FIG. 2a.—Diagram of apical di

FIG. 2 b-d.—Diagrams to show in the ambulacra, 2b, above ambitus; 2d, below

aries, in horizontal series pair is smaller than miliary in the other series of both columns never more than four

new species of *Echinotiara* from the same locality is allied the two silicified and iron-stained fragments of tests from *lenia smelliei* and ? *Hemicidaris bihinensis*, are too poorly preserved, but they also are probably from the same horizon. and implies a connection between the Somaliland sea and

de three new species which are described in the following presents a new genus, the exact relations of which are

consists, as described by Mr R. A. FARQUHARSON \* in his lie and an upper chalky white limestone. The lower limestone contained fossils are all more or less silicified and iron-stained echinoids in this state of preservation are necessarily that they are of Lower Eocene age. The following are

*Linthia* ? n. sp.

*Schizaster* ? sp. aff. *concinus*, Pér. and Gauth.

*Schizaster* ? sp. aff. *ournoueri*, Cotteau.

*Schizaster* ? sp. aff. *pyrenaicus*, Munier-Chalmas.

*Schizaster* cf. *gaudryi*, De Loriol.

Cretaceous age, *Pygaulus* being typically Cretaceous. either Cretaceous or Eocene, while *Plesiolampas* ?, *Periour* an Eocene age. *Schizaster gaudryi* is a Lower Eocene being nearly all questioned, have little weight separately, but reliable enough, and it also indicates a Lower this horizon were collected at localities in Eastern and

the limestone are as follows :—

*Linthia* sp. aff. *insignis*, Mérian.

*Schizaster* ? cf. *symmetricus*, Duncan and Sladen.

*Opissaster farquharsoni*, n. sp.

stone, excluding the specimens of *Sismondia* limestones, naliland. The *Sismondia* limestone is from Eastern and

*linthia* sp. aff. *insignis* and *Schizaster* ? cf. *symmetricus* Middle Eocene, while the indirect evidence of the other view.

with its silicified iron-stained fossils is so strikingly like the named by Professor GREGORY † in 1900), as to suggest that already stated, the cherty limestone, on the evidence of the

\* First Report on the Geol. and Min. Resources of Brit. Som., p. 14.  
ss. Corals and Echinids of Som.,” Q.J.G.S., vol. lvi, p. 26.

\* HAWKINS, 1920. “M

echinoids in the present collection, is Lower Eocene. The Middle Eocene age, assigned to the Auradli Limestone by the late R. B. NEWTON\* in 1905, was based on the occurrence of certain casts of large gastropoda which he determined as *Campanile*. Dr J. WEIR tells me that the affinities of the so-called *Campanile* are problematical; and that the inconclusive evidence of the other mollusca from the Auradli Limestone is not inconsistent with a Lower Eocene age.

The view that the Auradli Limestone is Lower Eocene renders it highly probable that the Allahkajid Limestone,† which was placed below the Auradli Limestone in the sequence based on the WYLLIE-SMELLIE collections, is part of the Middle Eocene, upper white limestone described by Mr FARQUHARSON. The echinoids from Allahkajid in the WYLLIE-SMELLIE collection indicated either a Lower or a Middle Eocene age for that limestone, while the Auradli Limestone, being then regarded as Middle Eocene, was believed to overlie the Allahkajid. Since the Auradli Limestone appears to be Lower Eocene, the Allahkajid Limestone is probably Middle Eocene, and should overlie the Auradli in the sequence.

## JURASSIC ECHINOIDEA.

### Family ACROSALENIIDÆ.

Genus ACROSALENIA, Agassiz, 1840.

? *Acrosalenia smelliei*, Currie.

*Acrosalenia smelliei*, Currie, 1925. *Monogr. Hunt. Mus.*, i, p. 53, pl. viii, fig. 5 a, b.

*Material*.—Two poorly preserved (silicified and iron-stained) incomplete tests (B.M., E. 18002-3) are very doubtfully referred to this species.

*Distribution*.—Bihin Lst., Bihendula : Deberaweina, W. Som.

Sub-genus METACROSALENIA, Currie, 1925.

*Acrosalenia* (*Metacrosalenia*) *pseudocidaroides*, Currie.

*A. (M.) pseudocidaroides*, Currie, 1925. *Loc. cit.*, p. 55, pl. viii, fig. 6 a, b.

*Material*.—One incomplete test, B.M., E. 18012.

*Dimensions*.—Diameter (D), 24.6 mm.; height (H), 15.8 ? mm.; H/D, .64.

*Distribution*.—Bihin Lst., Bihendula : Ida Kabeitah Hill, near Aurahu, Central Som.

This specimen differs from the holotype (Hunterian Museum, E. 735) in the apical system, having a different arrangement of suranal plates, and probably also in its surface being more nearly level. The height of the specimen cannot be measured exactly, but it is evidently slightly greater than that of the holotype. In the present specimen simple primary ambulacral plates are apparent from the apex to the ambitus.

*Pentagonal variety?*—One much worn specimen of a *Metacrosalenia* (B.M., E. 18013) from the same locality, is probably a variety of the above species. It apparently differs from the holotype in being larger, in being pentagonal in outline, and in having a different arrangement of suranal plates (of which there are three) in the apical system. This specimen is of interest also as showing that in *Metacrosalenia* the ambulacral plates are

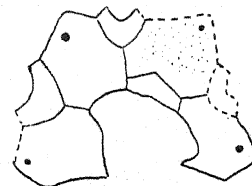


FIG. 1.—*Acrosalenia* (*Metacrosalenia*) *pseudocidaroides*, CURRIE. Diagram of apical disc of B.M., E. 18012.

\* NEWTON, 1905. "Tert. Fossils of Som.," *Q.J.G.S.*, vol. lxi, p. 160.

† See GREGORY, 1925. *Monogr. Hunt. Mus.*, vol. i, p. 5.



simple primaries to at least within a very short distance of the peristome. The pore-pairs are crowded just before the peristome. It differs from B.M., E. 18012 in the simple primary plates being more curved than they are in that specimen, an indication of the beginning of plate complexity (*vide* H. L. HAWKINS \*).

*Dimensions*.—Diameter (D), 26.0 mm.; height (H), 16.6 mm.; H/D, .64.

*Tumid variety?*—Portions of three tests, all much abraded and all from the above locality, may represent a tumid variety of this species. The simple primary ambulacral plates appear to be even more curved than those of B.M., E. 18013, and they interdigitate more with one another. B.M., E. 18015 is the most complete and has approximately the following dimensions: Diameter (D), 28.8 mm.; height (H), 22.4 mm.; H/D .77.

*Acrosalenia* (*Metacrosalenia*) *quadrिमिलiariis*, n. sp.

*Diagnosis*.—A *Metacrosalenia* in which the adapical quarter of the ambulacrum bears four vertical series of equal-sized miliaries (or small tubercles?). Beyond this point the miliaries of the two inner series decrease in size and increase in number, while the two main marginal series become larger adorally and definitely mamelonate. There are never more than four miliaries in irregular rows between the main series of tubercles.

*Material*.—Holotype. British Museum, E. 18011.

*Dimensions*.—Diameter (D), 23.5 mm.; height (H), 16.1 mm.; H/D, .69.

*Locality*.—Ida Kabeitah Hill.

*Description of Holotype*.—Test sub-globular, oral surface flat, and apical surface depressed. Edges high, steep, and rounded. Ambitus about the mid-height.

*Apical System*.—Pentagonal. Periproct to the posterior. Genital plates 1, 2, 3, and 4 large, 1 contiguous with 2, 2 with 3, and 3 with 4, their aboral edges outlining an angular space indicating the position of a suranal plate (or plates). Genital 5 small. The three anterior ocular plates exsert, the two posterior insert with respect to the periproct.

*Ambulacra*.—Narrow and sinuous, increasing very little in breadth towards the peristome. Pores large and oval with interpore granule; the pairs in simple, sinuous series until near the peristome, where they are arranged in oblique triplets. In the adapical quarter of the area (with the exception of the extreme apex) there are four vertical series of comparatively large equal-sized miliaries set in two series of twos, placed alternately (fig. 2*b*). Beyond this point, a miliary in one inner series (sometimes in column *a* and sometimes *b*) becomes smaller, and the corresponding miliary in the other inner series is replaced by two still smaller miliaries, in horizontal series with a main tubercle (fig. 2*c*). (Sometimes the inner miliary of the pair is smaller than the other, and sometimes they are of equal size.) Then the reduced miliary in the other inner column is also replaced by two smaller miliaries; the horizontal series of both columns become slightly curved and overlap so that there are often three and never more than four small miliaries in irregular rows between the main marginal series (fig. 2*d*).

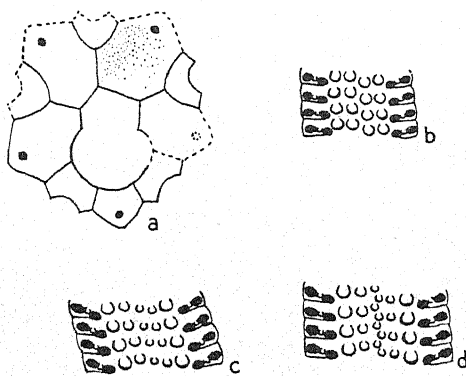


FIG. 2.—*Acrosalenia* (*Metacrosalenia*) *quadrिमिलiariis*, n. sp.

FIG. 2*a*.—Diagram of apical disc of holotype.

FIG. 2*b-d*.—Diagrams to show the tuberculation in the ambulacra. 2*b*, adapically; 2*c*, just above ambitus; 2*d*, below ambitus.

\* HAWKINS, 1920. "Morph. and Evol. of the Amb. in Ech. Holact.," *Phil. Trans. Roy. Soc., Ser. B*, vol. ccix, p. 396.

At the same time, the marginal series of miliaries increase in size adorally and become definitely mamelonate. Minute granules are sometimes interspersed. The above arrangement prevails in the greater part of the area, the inner miliaries becoming smaller and the marginal tubercles more outstanding adorally. At the peristome, occupying a length of about  $\frac{1}{6}$ th of the area, there are four pairs of comparatively large tubercles.

Interambulacra.—Eight to nine plates in a column. Ultimate plate in column *a* very small. The ultimate in *b* and the penultimate in *a* are high, and covered with miliaries and bear a small tubercle (usually non-scribulate) situated near to the adoral and to the adradial sutures. The other plates are large and high, and bear fully developed tubercles, each occupying most of the plate. In these main tubercles large perforate mamelons rest on platforms with 11–12 crenellæ, and the boss, which dies away in the scribule, has a slightly concave slope. The scribules of the adapical tubercles are circular and contiguous; in the adoral tubercles the scribules become confluent. The scribicular rings of tubercles extend along the extreme margin of the adradial suture, and are separated from the interradial suture only by occasional minute granules.

Peristome.—Large. Branchial incisions large. Ambulacral slightly wider than interambulacral lobes.

*Affinities.*—This species is very like *A. (M.) pseudocidaroides*, Currie (1925, *loc. cit.*, p. 55, pl. viii, fig. 6 *a, b*), so much so, that one thought it might be another variety of that species. As the single specimen available differs from *A. pseudocidaroides*, not only in dimensions and in the arrangement of suranal plates in the apical system, but also in the tuberculation of the ambulacra, it seems better to regard it as a distinct species for the present at least.

This species may be distinguished from the species *A. pseudocidaroides* by its ambulacral areas. They are slightly narrower than those of *A. pseudocidaroides*, and they increase in breadth very little adorally, less than is the case in that species. The small miliaries between the main tubercle series in *A. pseudocidaroides* (described as granules, Currie, 1925, *loc. cit.*) are relatively smaller and more numerous than those in the present species, in which there are never more than four between the main tubercles; in *A. pseudocidaroides* there may be as many as five. The species *A. quadrimiliaris* is characterised by having four series of comparatively large equal-sized miliaries in the adapical quarter of the ambulacrum, whereas in *A. pseudocidaroides* the arrangement of prominent main tubercles with small intermediate miliaries is continuous to the apex of the area.

#### Genus RECROSALENIA, Currie, 1925.

##### *Recrosalenia somaliensis*, Currie.

*Recrosalenia somaliensis*, Currie, 1925. *Loc. cit.*, p. 48, pl. viii, fig. 1 *a–e*.

*Material.*—One specimen, B.M., E. 18008. It is incomplete, and the greater part of the apical surface is concealed by matrix.

*Dimensions.*—Ant.-post. diameter, 22.0 mm.; trans. diam., 20.3 mm.; height, 9.8 ? mm.

*Distribution.*—Bihin Lst., Bihendula; Biyo Dader Tug or Well, Gadabursi, W. Som.

*Remarks.*—This specimen adds to what is known of the species. It differs from the holotype (Hunterian Museum, E. 764) in several points. It is elliptical in ambital outline, whereas the holotype is sub-pentagonal. Its longer diameter appears to be in the direction of the antero-posterior axis, whereas in the holotype the transverse diameter is the longer one. Another difference is perforation of the extreme adoral tubercles, apparent in one of the ambulacral areas of B.M., E. 18008. In the holotype, as stated in the description

(CURRIE, 1925, *loc. cit.*), small imperforate tubercles and miliaries occur alternately just at the peristome. In one of the ambulacra of B.M., E. 18008 the extreme adoral main tubercle in both columns *a* and *b* is perforate (crenulate? also), and in column *a*, adoral to the first main tubercle, is a smaller perforate tubercle where one expected a miliary. To the diagnosis of *Recrosalenia* I would add that the extreme adoral tubercles may be perforate.

### Family HEMICIDARIDÆ.

Genus HEMICIDARIS, Agassiz, 1840.

? *Hemicidaris bihinensis*, Currie.

*Hemicidaris bihinensis*, Currie, 1925. *Loc. cit.*, p. 59, pl. ix, fig. 3 *a, b*.

*Material*.—One poorly preserved (silicified and iron-stained) fragment of a test (B.M., E. 18004), which includes the greater part of an ambulacrum and an interambulacrum.

*Distribution*.—Bihin Lst., Bihendula; Deberaweina, W. Som.

### Family ?

Genus FARQUHARSONIA, n. gen.

*Diagnosis*.—A Diademoid, with uniserial pore-pairs and simple primary ambulacral plates, at least adapically (all?); with small main ambulacral tubercles situated between two plates of each triad, and small secondaries between the main tubercles. Apical disc small. Main interambulacral tubercles perforate, non-crenulate, situated centrally with respect to the transverse sutures of the plates. Secondary interambulacral tubercles small, occurring interradially and adradially to the main tubercle. Gill-slits long and narrow, the interambulacral margin bordered by a triangular area, which is a continuation of the interambulacral lobe.

*Farquharsonia somaliensis*, n. sp.

*Material*.—Holotype: British Museum, E. 18006. Paratype: British Museum, E. 18007. The holotype is somewhat crushed and broken, and has matrix adhering in places, while the surface ornament of the test, where exposed, is slightly abraded. In the paratype the whole surface is much abraded, and most of the oral surface is destroyed.

*Dimensions*.—The diameter of the holotype is about 29.5 mm. and its height about 16 mm. The diameter of the paratype is about 32.2 mm.

*Locality*.—Biyo Dader Tug or Well.

*Description of the Species*.—Test circular (to slightly pentagonal? in holotype) in ambital outline. Ambitus probably about one-third of the height above the base plane. Oral surface probably almost flat, slightly concave towards the peristome; apical surface hemispherical, depressed.

*Apical System*.—Small. Not clear in either of the specimens. Its antero-posterior diameter in the holotype is about 5 mm., and that of the paratype about 6 mm., i.e. .17 and .18 of the diameter of the test. The periproct large and situated to the posterior in the system. The genital plates comparatively large, the right anterior largest and probably entirely covered with madreporic pores. Ocular plates small; the three anterior exsert and the right posterior insert with respect to the periproct (left posterior not visible).

*Ambulacra*.—Narrow. The holotype does not show the nature of the ambulacral plates, but in the paratype they are apparently simple primaries, at least adapically. Pore-pairs



uniserial, departing only slightly from a straight line, and continuous thus to the peristome. The inner pore is circular, the exterior oval and obliquely set, separated by a large interporal granule. Where the test is worn as in the paratype, both pores appear more or less circular. Ambulacral tubercles small, in series along the extreme margins of the pore-fields, one to every three pairs of pores, situated between the first and second pairs of every triad, and, where the plating is visible, between two plates. In the adapical half of the area there are no secondary tubercles, the perradial tract being covered with a fine granulation or shagreening. In the adoral half of the area, very small secondary tubercles are developed, and the fine shagreening of the adapical half is replaced, or more probably masked, by a larger and more sparse granulation. The small secondary tubercles seem to occur in twos, in horizontal series, alternating with the main tubercles, the adradial one of the pair being in line with the main tubercle series.

Interambulacra.—Wide. Plates low and wide. About 16 in a column in the holotype. Tubercles situated slightly adradially to the centre of the plates. The adapical tubercles (6-7 in holotype) are small and non-scribulate, and the plates are entirely covered by shagreening similar to that of the ambulacral areas. The tubercles of the ambital plates are large and fully developed; they become gradually smaller adorally, the extreme adoral tubercles being very small. The abrupt change from the undeveloped adapical tubercles to those that are fully developed is striking and occurs at, or slightly above, the ambitus. The large scribulate tubercles are all more or less worn down, but they probably had small perforate mamelons on comparatively large smooth platforms, small bosses with steeply concave sides ending in well-marked basal terraces. Scribules wide, circular, and contiguous in the adoral tubercles, but in the ambital tubercles distinct and adjacent. Faint crenulations are visible in some of the small adoral tubercles. Scribicular rings composed of numerous (25-28) minute tubercles. In the holotype, small secondary tubercles are apparent in the adoral plates, adradially and interradially. The adradial secondaries form a roughly vertical series, slightly arcuate with the scribules. The arrangement of the interradial secondaries is not clear. On one plate there are five (2 of them larger than the others), arranged at the angles of a pentagon, and on another plate there are only two arranged in vertical series. In each column of plates, the plate bearing the last scribulate tubercle (fig. 3b) (which is the largest of the series, and is just at, or slightly above, the ambitus) differs from the adoral plates in the absence of secondary tubercles; or, if present, they are indistinguishable from numerous small miliaries, which occur on the extra-scribicular surface near the scribicular ring. The shagreening of the adapical plates is probably present in the adoral plates also, but is not so obvious, as small granules are sparsely and irregularly scattered among the secondaries.

Peristome.—Probably in a concavity of the base. Interambulacral lobes wide and with straight margin at the peristome. The gill-slits (three visible in holotype) are long and parallel-sided, and the interambulacral edge is thickened by a slight ridge. Extending from the top of the gill-slit towards the peristome, and at an angle to the direction of the slit, is

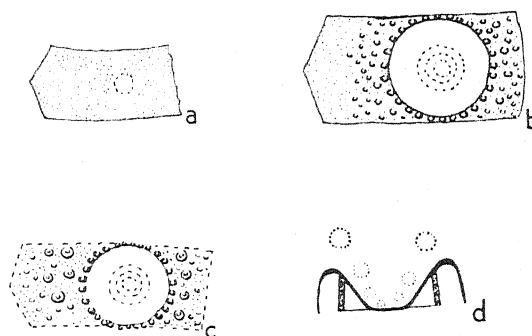


FIG. 3.—*Farquharsonia somaliensis*, n. gen. and sp.

FIGS. 3 a-c.—Diagrams of interambulacral plates of holotype. 3a, adapical; 3b, ambital, the plate bearing the last scribulate tubercle; 3c, below the ambitus.

FIG. 3d.—Diagram of extreme adoral portion of an interambulacral area in holotype showing the gill-slits.

another slight ridge, two of these in an interambulacrum meeting around the adoral extremity of the area. The interambulacral series of tubercles extend adjacent to these inner ridges, and the small triangular space between the inner ridge and the ridged edge of the gill-slit is slightly depressed and bears a few granules. The appearance of the interambulacral lobe suggests that the inner ridge is the margin of an earlier gill-slit, and that stereom formation along this margin has reduced the original slit to its present parallel-sided shape (fig. 3*d*).

*Affinities.*—The unusual character of this species has necessitated the creation of a new genus, which I have called *Farquharsonia*, after the collector of the specimens. In *Farquharsonia*, as already stated, the adapical ambulacral plates are simple primaries, and the ambulacral tubercles are situated between the first and second plates of every triad. This arrangement is characteristic of *Orthopsis*, but it occurs also in the adapical plates of the Calycina and the Diadematidae, and is, according to Professor H. L. HAWKINS,\* preliminary to the formation of triads. One cannot make out from the two specimens available the nature of the ambital and adoral plates. The arrangement of the pore-pairs in simple series from the apex to the peristome, however, and the situation of the tubercles between two pore-pairs of every three, render it highly probable that the plates in those areas are simple primaries also.

A first examination of the specimens of *Farquharsonia* suggested that they might belong to the genus *Orthopsis*. The small apical disc, the simple series of pore-pairs from apex to peristome, the simple primary ambulacral plates (although only visible adapically), the situation of the ambulacral tubercles and the shagreening of the surface of the test are points which lead to this view. The ambulacral tubercles, both main and secondary, are, however, smaller than is usual in *Orthopsis*, and the tuberculation of the interambulacral areas also does not agree with that genus. As pointed out by Dr F. A. BATHER,† the main interambulacral tubercles in *Orthopsis* are adoral in position on each plate, and the secondary tubercles, which are large, are adapical. According to the same writer, another feature of *Orthopsis* is the absence of convergence of the main interambulacral tubercles at the peristome in conjunction with the wide, straight, interambulacral lobe. In the present species the main interambulacral tubercles are situated centrally with respect to the transverse sutures of the plates, and the secondaries are very small. The main series are convergent, almost touching at the peristome, so that very little resorption has taken place. Nevertheless, the species agrees with *Orthopsis* in having a wide, straight, interambulacral lobe; but whereas that of *Orthopsis* is the result of resorption, in this species it appears to be the result of stereom formation, producing the triangular areas on the interradian margins of the gill-slits.

The present species also resembles *Hemipedina*, the arrangement of the tubercles in the adoral interambulacral plates being somewhat similar to that in such species as *H. perforata* Wright, *H. waterhousei* Wright, and *H. tuberculosa* Wright, in which the secondary tubercles are small and even difficult to detect. The interambulacral plates in *Farquharsonia* differ, however, in being much lower and wider than those in the above species of *Hemipedina*. The small size of the apical disc in *Farquharsonia* is another point of difference from *Hemipedina*, in which the apical disc is large, being usually about one-third of the diameter of the test, although it may be more or slightly less. In the present species the apical disc is about 1/18 of the diameter of the test.

In the sparse tuberculation of the adapical interambulacral plates, the species differs from both *Hemipedina* and *Orthopsis*, but this is probably only a specific character. The upper mid-zonal plates of the interambulacra (those just at or slightly above the ambitus)

\* HAWKINS, 1920. *Loc. cit.*, p. 389.

† BATHER, 1909. *Triassic Echinoderms of Bakony*, p. 108.

are less elaborate than more adoral plates, so the species is probably regressive. In its unusual gill-slits also *Farquharsonia* differs from both *Hemipedina* and *Orthopsis*.

In discussing the genus *Orthopsis*, Dr BATHER (*loc. cit.*, pp. 107-109) pointed out that that genus is less primitive than would appear from the character of the ambulacra, and in a concluding hypothesis (*loc. cit.*, p. 116) setting forth the evolution of various genera, it is stated that *Orthopsis* arose as a branch from *Hemipedina*, a branch with enlarged secondary tubercles. It is interesting, therefore, to find that in the new genus *Farquharsonia*, the main features are those of a possible link between these two genera. *Farquharsonia* might be described (apart from its unusual gill-slits) as an *Orthopsis*, in which the interambulacra are of the more primitive type of *Hemipedina*. It is possible that its systematic position is somewhere in the line or lines of descent from *Hemipedina* towards *Orthopsis*, although this probably implies that the simplicity of the ambulacra in *Farquharsonia* is secondary. If one regards *Hemipedina* as ancestral to *Farquharsonia*, and if the ambulacra of *Farquharsonia* are as simple as one supposes, then their simplicity must be a reversion from the *Hemipedina* ambulacrum to the more primitive condition. In the case of *Orthopsis*, Dr BATHER (*loc. cit.*, p. 108) regarded the ambulacrum as not a simple reversion, but as a step towards increasing the number of tubercles in the area. In *Farquharsonia*, also, there are secondary tubercles in the ambulacra, but all the ambulacral tubercles are small, and there is no reason, in this case, to connect them with a reversion of the pore-pairs to straightness.

An alternative to the above view of the origin of *Farquharsonia* is that *Farquharsonia* and *Hemipedina* are derived from a common *Hemipedina*-like ancestor with uniserial pore-pairs and simple primary plates; and that while the *Hemipedina* branch evolved to a stage of more complex ambulacral plating, the *Farquharsonia* branch retained its simple ambulacra and progressed in the direction of the present *Farquharsonia*. Among known genera the Liassic genus *Archæodiadema*, J. W. Gregory (1896, *Geol. Mag.*, p. 317), regarded by later writers (J. LAMBERT,\* 1900, and F. A. BATHER, 1909, *loc. cit.*, p. 104) as synonymous with *Hemipedina*, is the only one which might fit the case. Its ambulacral plates are not all simple primaries, but its pore-pairs are uniserial (as in *Farquharsonia*, departing only slightly from a straight line); at the ambitus, the ambulacral tubercles are situated between two plates of each triad, while the third plate of the triad bears a small secondary tubercle. In these respects *Farquharsonia* agrees with *Archæodiadema*; they differ in the absence of secondary interambulacral tubercles in *Archæodiadema* and the large size of its apical disc. Before arriving at any definite conclusion as to the systematic position of *Farquharsonia*, one would have to know the nature of its ambital and adoral ambulacral plates.

The gill-slits of this species distinguish it from both *Hemipedina* and *Orthopsis*, and indeed from other Jurassic and Cretaceous genera. Certain species (from the Miocene of Algeria), figured by POMEL † and referred by him to the genus *Anapesus*, Holmes, 1860, show a somewhat similar triangular border to the gill-slits associated with similar long, narrow slits. In this respect *A. serialis* (*loc. cit.*, p. 303, C, pl. iv, figs. 1-7) is very similar to *Farquharsonia somaliensis*. In *A. maurus* (*loc. cit.*, p. 302, C, pl. vii) the triangular area is smaller. In *A. angulosus* (*loc. cit.*, p. 305, C, pl. vi) the triangular area appears to extend across the gill-slit, cutting off a part of it from the peristome. The figures of *Oligophyma cellensis*, Pomel, and *O. oranensis*, Pomel (*loc. cit.*, p. 307, pl. x), also show somewhat similar triangular areas bordering the gill-slits. AGASSIZ ‡ regarded *Anapesus* as synonymous with

\* LAMBERT, 1900. "Étude sur quelques Echinides de l'Infra-Lias et du Lias," *Bull. Soc. Sci. Yonne*, vol. liii, pt. 2, p. 29.

† POMEL, 1887. *Paléont. de l'Algérie*, fasc. 2, livr. 2, Echinod., p. 297.

‡ AGASSIZ, A. "Revision of the Echini," *Mem. Mus. Comp. Zool. Harvard*, vol. iii, 1872-74.

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the recent *Toxopneustes*. According to J. LAMBERT,\* the species referred by POMEL to *Anapesus* do not belong to that genus but should be left with *Schizechinus*, Pomel, 1869, which he (J. LAMBERT) regarded as a sub-genus of *Toxopneustes*. Furthermore, he considered the two species which POMEL referred to *Oligophyma* as really belonging to the genus *Anapesus*. COTTREAU† removed only POMEL's species *angulosus* and *serialis* to *Schizechinus*, regarding both *Schizechinus* and *Anapesus* as sub-genera of *Echinus*. Discussion of these genera is unnecessary here.

It is of interest to note that in at least some species of the recent *Toxopneustes*, *Hipponœ*, *Tripneustes*, and *Pseudoboletia*, which have long, narrow gill-slits, there is, at the interambulacral margin of the slits, a structure which shows some resemblance to that in the Jurassic *Farquharsonia* and in the Kainozoic *Anapesus* or *Schizechinus*. In these species the rounded interambulacral lobe has, on each side, a small wedge-shaped piece which externally has the appearance of a triangle, usually an extremely elongated one. Sometimes the marginal triangular area is so elongated as to be little more than a thickening along the interambulacral margin of the slit (as in *Hipponœ esculenta* (Leske)), but in others again it is larger, approaching in shape that observed in *Farquharsonia* and *Anapesus* (e.g. *Pseudoboletia indiana* (Mich.)), in which, according to AGASSIZ,‡ "the interambulacral lips of the cuts (are) quite well developed". It would seem, therefore, that the triangular areas in *Farquharsonia* are probably intensifications of a normal thickening of the interambulacral margins of the gill-slits. This, of course, could only occur in forms in which the original slit is very large. The advantage of the thickening was, no doubt, a strengthening of the long interambulacral lobe at the peristomial membrane, and where, as in *Farquharsonia*, the thickening is such as to produce a wide interambulacral lobe, it probably provided a wider, stronger area for the attachment of the protractor muscles of the jaws.

#### Family DIADEMATIDÆ.

Genus ECHINOTIARA, Pomel, 1883.

*Echinotiara somaliensis*, n. sp.

*Diagnosis*.—An *Echinotiara* in which the pore-pairs are arranged in slightly oblique triplets from the peristome to within a short distance of the apical disc. The interambulacral plates, with the exception of the extreme adapical plates, are very low and wide. The adapical ambulacral and interambulacral tubercles are very small, being only slightly larger than the miliaries which cover the plates; the miliaries comparatively large, homogeneous, and tending in the interambulacral plates to a rough arrangement in horizontal rows, especially in the ambital plates. In the adoral plates, where the tubercles are larger and secondaries present, the miliaries are slightly smaller.

*Material*.—Holotype: British Museum, E. 18009. The peristome and the greater part of the oral surface are obscured by adhering matrix, and the surface of the test worn and polished.

*Dimensions*.—Diameter (D), 15.9 mm.; height (H), 9.3 mm.; H/D, .58.

*Locality*.—Biyo Dader Tug or Well.

*Description of the Holotype*.—Test small, circular in ambital outline; ambitus slightly below the mid-height; oral surface almost flat (?), apical surface hemispherical, depressed.

*Apical System*.—Pentagonal. Periproct large, slightly to the posterior. The two

\* LAMBERT, 1907. "Descr. des Echinides foss. de la Prov. de Barcelone," *Mém. Soc. Géol. France*, Pal. 14, No. 24, fasc. 2-3, p. 67.

† COTTREAU, 1913. *Les Echinides du Bassin méditerranéen*, Ep. Neogene, p. 48.

‡ AGASSIZ, *loc. cit.*, p. 456, pl. va, fig. 8.

anterior genital plates largest. The ocular plates small, the three anterior exsert with respect to the periproct; the outlines of the two posterior oculars not clear.

**Ambulacra.**—Narrow. Pore-fields narrow. Pore-pairs in slightly oblique triplets, arranged on each plate in slightly arcuate triplets, the adoral pair nearest the perradial suture. Ambulacral plates compound, of simple diademoid type. Perradial and adradial sutures slightly depressed. The tubercles are situated on the margins of the pore-fields; they are small on the apical surface but larger on the oral surface. Miliaries are irregularly scattered over the plates and are so large as to render the small, worn, adapical tubercles not readily distinguishable from them.

**Interambulacra.**—About twice the breadth of the ambulacra. Interradial suture in a depression especially adapically. Plates low and wide, about seventeen in a column. Plates slightly arched in two directions, very little from the adoral to the adapical transverse sutures and more from the adradial to the interradial suture. This is most marked in the plates just above the ambitus. The highest point of each plate corresponds to the position of the main tubercle which is situated slightly eccentrically towards the interradial and also towards the adoral suture. The tubercles are very small above the ambitus but are larger below it. The adapical plates with small main tubercle bear no secondary tubercles but are covered with miliaries similar to those in the ambulacra. Their arrangement in the extreme adapical plates is irregular, but towards the ambitus there appears to be a rough arrangement in horizontal rows, three rows on each plate. On the plates below the ambitus, the main tubercles are larger and secondary tubercles are also developed, one situated on the interradial side and one (in some cases two) on the adradial side of the main tubercle. Miliaries, slightly smaller than those in the adapical plates, occur in irregular rows on these adoral plates also and very minute granules are also interspersed. 10–11 adapical plates bear small main tubercles, and there are probably 6–7 adoral plates with large main tubercles and secondaries also.

**Peristome.**—Unknown.

**Affinities.**—*Echinotiara bruni*, better known as *Echinodiadema bruni*, Cotteau,\* from the Bathonian of Niort, France, is the genotype of this rare genus.† The specimen under consideration seems to belong to the same genus. The arrangement of the pore-pairs in slightly oblique triplets, the compound diademoid plates, the marginal ambulacral tubercles, the small adapical interambulacral tubercles situated on the highest points of the plates, and the sudden increase of tuberculation on the oral surface, both as regards size and number of tubercles, form a striking enough assemblage of their common characters. *E. somaliensis* appears to differ from *E. bruni* in the following respects:—(1) In *E. somaliensis* the pore-pairs are arranged in arcuate triplets until at least very near to the apical disc, whereas in *E. bruni* the adapical pore-pairs tend to be directly superposed, the arcuation becoming apparent

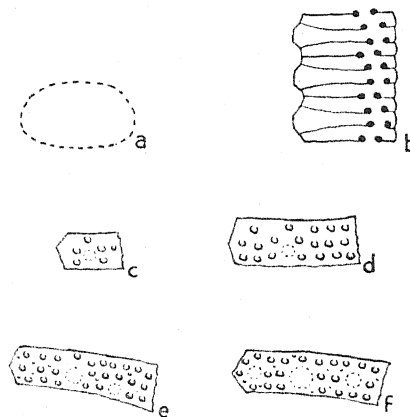


FIG. 4.—*Echinotiara somaliensis*, n. sp.

FIG. 4a.—Profile outline of holotype.

FIG. 4b.—Diagram of portion of an ambulacrum.

FIGS. 4 c-f.—Diagrams of interambulacral plates of holotype: 4c, extreme adapical; 4d, just above ambitus; 4e, ambital; 4f, below ambitus.

\* COTTEAU, 1869. *Rev. and Mag. de Zool.*, ser. 2, vol. xxi, p. 238, pl. xli; also in *Echinides nouv. ou peu connus* (1859–80), ser. i, p. 142, pl. xix, figs. 1–5.

† The real *Echinodiadema* is VERRILL's recent genus (1867. "Notes on Radiata," *Trans. Conn. Acad.*, i, p. 295); COTTEAU's *Echinodiadema bruni* was placed by POMEL (1883. *Classific. et Genera des Echinides*, p. 82) in *Echinotiara*.

towards the ambitus. (2) *E. somaliensis* has a greater number of interambulacral plates in a column and they are lower and wider than those of *E. bruni*. (3) The interambulacral tubercles of *E. somaliensis* are situated on the highest point of the slightly arched interambulacral plates; whereas in *E. bruni* the tubercles are described as situated on small swellings (renflements) on the plates. (4) The miliaries covering the plates of *E. somaliensis* are larger and more numerous than the "granules" of *E. bruni*, and in the interambulacral areas they tend to an arrangement in more or less regular horizontal rows.

So far as I know, the only other species of *Echinotiara* is *E. parkeri*, Fourtau,\* from the Aptian of Egypt. It differs from both the genotype and the present species in having rudimentary series of secondary tubercles in the interambulacra.

COTTEAU (1869, *loc. cit.*) likened his *Echinodiadema* to *Psammechinus*, Agassiz, and placed it in the *Echinidæ*, although he regarded it as being on the border line between the *Diadematidæ* and the *Echinidæ*. As his figures of the genotype (*loc. cit.*) show, however, the ambulacral plates are of simple diademoid type and not echinid; hence it does not belong to the *Echinidæ*. It is really on the border between the *Diadematidæ* and the *Pedinidæ*, the genera of which (*Pedinidæ*) COTTEAU included in the *Echinidæ*. P. M. DUNCAN † placed *Echinodiadema* (of COTTEAU) in the *Diadematidæ*, regarding it merely as a sub-genus of *Diadema*. In this report, following the classification of Dr J. W. GREGORY,‡ *Echinodiadema* (of COTTEAU) is regarded as a genus in the *Diadematidæ*. The tendency towards the *Pedinidæ* is more marked in the present specimen than in the genotype, *Echinotiara bruni*, the arrangement of the pore-pairs in *E. somaliensis* being a step farther in the direction of that family. The pore-pairs in *E. somaliensis* appear to be set closer together; they are arranged in oblique triplets to at least within a short distance of the apical disc, and the triplets are slightly more oblique. It may be that they are triserial right up to the apical disc.

### Family PEDINIDÆ.

Genus STOMECHINUS, Desor, 1858.

*Stomechinus* aff. *microcyphus*, Wright.

*Stomechinus microcyphus*, Wright, 1858. *Monogr. Brit. Foss. Echinod. Ool. Format.*, i, Echinoidea, p. 213, pl. xv, fig. 1 a, b.

" " Desor, 1858. *Synop. Echinides Foss.*, Suppl., p. 434.

" " Cotteau, 1884 and 1885. *Pal. Franc.*, Terr. Jurass., 10, Echinides Reg., p. 763, pl. 478, figs. 2-5, and p. 894, pl. 514, figs. 1-12.

*Material*.—One specimen (B.M., E. 18026) the surface of which is worn and decorticated.

*Dimensions*.—Diameter (D), 28.6 mm.; height (H), 16.8 mm. approx.; H/D, .59.

*Locality*.—Bihendula.

*Remarks*.—This specimen is very near to the species *S. microcyphus* Wright from the Bathonian of England and France. It has four series of tubercles in the ambulacra at the ambitus and twelve in the interambulacra, and the tuberculation appears to be of the same type as in that species.

Dr. F. L. KITCHIN has been kind enough to enable me to borrow a specimen of *S. microcyphus* in the collection of the Geological Survey Museum, Jermyn Street (No. 32319 from the Great Oolite of Minchinhampton), which, he has informed me, Professor HAWKINS thinks may quite possibly be the type-specimen of WRIGHT. The present specimen from Somaliland

\* FOURTAU, 1921. "Catal. Invert. Foss. de l'Egypte," *Geol. Surv. Egypt*, Pal. Ser. No. 5, p. 48, pl. v, fig. 7.

† DUNCAN, 1889. "Revision of the Gen., etc., of the Echinoidea," *Journ. Linn. Soc., Zool.*, xxiii, p. 64.

‡ GREGORY in BATHER, 1900. *A Treatise on Zoology*, Ed. RAY LANKESTER, pt. iii, Echinoderma.



differs from No. 32319 of the Survey Museum in being of large diameter and in being slightly more depressed, while more essential differences are the lower, wider interambulacral plates and the smaller peristome of the Somaliland specimen.

As remarked by both WRIGHT and COTTEAU, *S. microcyphus* strongly resembles *Polycyphus normannus* Desor, but *P. normannus* differs in having a greater number of interambulacral tubercles at the ambitus and in their more regular arrangement. Two specimens from Somaliland, which I described as *Polycyphus* cf. *normannus* (Currie, *loc. cit.*, 1925, p. 62, pl. ix, fig. 6), differ from the present specimen, E. 18026, in these respects, and also in being more depressed and of larger diameter.

### Family PYGASTERIDÆ.

#### Genus HOLECTYPUS, Desor, 1842.

##### *Holctypus*, sp. indet.

*Material*.—One much worn specimen, B.M., E. 18010. The tuberculation of the test is destroyed and the peristome is concealed by matrix.

*Dimensions*.—Ant.-post. diam., 20.5 mm.; trans. diam., 19.6 mm.; height, 9.3 mm.

*Locality*.—Biyo Dader Tug or Well.

*Remarks*.—The periproct is large and pyriform and extends from the margin to near the peristome as in *H. depressus* (LESKE).<sup>\*</sup> One naturally compares the specimen with *H. depressus*, one of the commonest of Jurassic *Holctypi*, but, considering its state of preservation, it could equally well be likened to *H. corallinus*, D'ORB.<sup>†</sup> or *H. arenatus* (DESOR),<sup>‡</sup> or possibly other species of *Holctypus* in which the form is depressed and the periproct extends from near the peristome to the margin.

##### *Holctypus*, n. sp.

*Material*.—One poorly preserved specimen, B.M., E. 18005.

*Dimensions*.—Diameter (D), 32.3 mm.; height (H), 15.5 mm.; H/D, 0.48.

*Locality*.—Biyo Dader Tug or Well.

*Description of Specimen*.—The upper surface of E. 18005 is bluntly conical, the edges rounded, and the lower surface almost flat with the peristome in a small central depression. The peristome is evidently very small. The outline of the periproct is incomplete, but from what is visible one would say it is narrowly elliptical and situated equidistant from peristome and margin; its length is probably equal to about half the distance between the peristome and the margin. The tuberculation is of the *Pygaster*-type described by Professor H. L. HAWKINS.<sup>§</sup> It can only be observed on two plates situated just below the ambitus; their surface is worn and cracked,

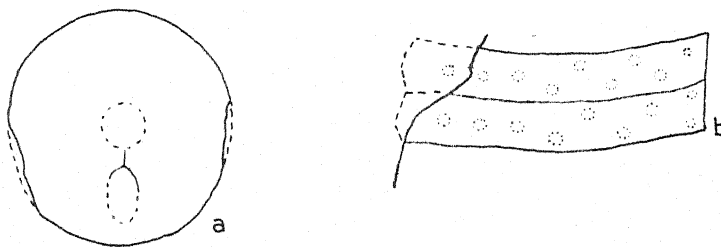


FIG. 5.—*Holctypus*, n. sp.

FIG. 5a.—Diagram of oral surface of B. M., E. 18005.

FIG. 5b.—Diagram to show tuberculation of interambulacral plates just below ambitus.

<sup>\*</sup> LESKE, 1778. *Addit. ad Kleini dispos. Echinod.*, p. 164, pl. xl, figs. 5-6.

<sup>†</sup> D'ORBIGNY, 1850. *Prod. de paléont. strat.*, t. 11, p. 26.

<sup>‡</sup> DESOR, 1842. In AGASSIZ, *Monogr. des Echinod.*, iii, Galérites, p. 68, tab. ix, figs. 11-13.

<sup>§</sup> HAWKINS, 1911. "The Tuberculation of the *Holctypoida*," *Geol. Mag.*, n.s., dec. v, vol. viii, p. 442.

but one can make out the horizontal row of tubercles on the interradial and the oblique rows on the adradial side of the main tubercles. There appear to be three tubercles in the horizontal row on each plate, but there may have been four originally. The ambulacral areas probably bear six vertical series of tubercles.

*Affinities*.—In the position of the periproct and the *Pygaster*-type of tuberculation, the specimen E. 18005 is similar to *H. choffati*, DE LORIOI,\* from the Lusitanian of Portugal. *H. choffati* differs in being very much larger and more depressed and in its ambulacra being relatively much narrower.

The present species agrees with *H. planus* (AGASSIZ) † from the Oxfordian of France in its form and in the position of the periproct, although that of the present specimen is probably narrower than that of *H. planus*. *H. planus* is a much smaller species than the present and the tuberculation is probably not of the same type.

#### Family CASSIDULIDÆ.

Genus CLYPEUS, Leske, 1778.

*Clypeus wylliei*, Currie.

*Clypeus wylliei*, Currie, 1925. *Loc. cit.*, p. 63, pl. x, figs. 1 a-c.

*Material*.—One specimen, B.M., E. 18028.

*Distribution*.—Bihin Lst., Bihendula.

Genus PYGURUS, Agassiz, 1839.

*Pygurus smelliei*, Currie.

*Pygurus smelliei*, Currie, 1925. *Loc. cit.*, p. 67, pl. x, fig. 5 a-c.

*Material*.—One specimen, B.M., E. 18027.

*Distribution*.—Bihin Lst., Bihendula.

*Pygurus cf. depressus*, Ag. var. *somaliensis*, Currie.

*P. depressus*, var. *somaliensis*, Currie, 1925. *Loc. cit.*, p. 65, pl. x, figs. 4 a-c.

One somewhat flattened specimen of *Pygurus* (B.M., E. 18029) from Bihendula may possibly belong to the above species, but it differs from all the other specimens of the variety that I have examined. It is larger than the other specimens, its length being about 70.5 mm. Its main difference lies in its very wide ambulacral petals and the relatively very wide pore-fields. Furthermore, the petals are raised above the level of the interambulacra. As previously stated (CURRIE, 1925, *loc. cit.*, p. 67) the ambulacral petals vary in this species, the breadth of the perradial tract, as compared with the pore-fields, varying considerably, and it is possible that the specimen under discussion is an extreme form of this variation. As the floscelle and the greater part of the oral surface are concealed by matrix, detailed comparison is impossible.

\* DE LORIOI, 1890. "Descr. de la Faune Jurassique du Portugal," *Commiss. Travaux Geol. du Portugal*, fasc. i, Echinides, p. iii, pl. xx, figs. 1-2.

† AGASSIZ, 1840. *Catal. Syst. Ectyp. Echinod. Mus. Neoc.*, p. 7; also DESOR, 1842. *Loc. cit.*, p. 64, tab. 9, figs. 1-3.

Genus BOTHRIOPNEUSTES, R. Fourtau, 1924.

*Bothriopneustes somaliensis* (Currie).

Syn. *Clypeobrissus somaliensis*, Currie, 1925. *Loc. cit.*, p. 69, pl. x, figs. 6 a-c.

*Material*.—Eight specimens, B.M., E. 18018–E. 18025.

*Dimensions*.—Length, 47–31.3 mm.; breadth, 0.93–0.95 of the length; height, .43–.47 of the length.

*Distribution*.—Bihin Lst., Bihendula.

*Affinities*.—The genus *Bothriopneustes* Fourtau is described in a posthumous 1924 publication of the late R. FOURTAU\* on Jurassic Echinoids from North Sinai. Not being cognisant of this work, I described a new genus *Clypeobrissus*, based on specimens of the present species from Somaliland in the Hunterian Museum, Glasgow University. I have since found that *Clypeobrissus* is the same as R. FOURTAU's *Bothriopneustes* and the name *Clypeobrissus* must therefore be suppressed.

The genotype is *Bothriopneustes lamberti* Fourtau (*loc. cit.*, p. 28, pl. ii, fig. 5) with which the Somaliland species is no doubt congeneric, and from which it is also quite distinct. *B. lamberti* is a narrower and also a rather more depressed form than *B. somaliensis*; it is also more contracted towards the posterior, being sub-rostrate. Furthermore, the pore-fields of the petals are relatively narrower than in *B. somaliensis*.

On the other hand, *B. somaliensis* is extremely like *Bothriopneustes orientalis* Fourtau (*loc. cit.*, p. 29, pl. v, fig. 9–13) from the same locality as *B. lamberti*. It is even possible that comparison of actual specimens might prove them to be the same, but in the meantime, as there appear to be several points of difference, it is better to keep them distinct.

The figured specimen of *B. orientalis* (*loc. cit.*, pl. v, figs. 9–12) is relatively narrower than *B. somaliensis*, and, no doubt, is the specimen of which the dimensions are given, showing that the breadth is .83 of the length. In *B. somaliensis* the outline of the test is more nearly circular, the breadth varying from .91 to .95 of the length, .95 being the commonest proportion. (This statement is based on the specimens in the Hunterian Museum as well as those in the present collection.) FOURTAU, however, gave dimensions of another specimen of *B. orientalis*, in which the breadth is .91 of the length, a proportion near that of *B. somaliensis*. In *B. somaliensis*, the height varies from .43–.49 of the length. In the two specimens of *B. orientalis* already referred to, for which FOURTAU gave dimensions, the height is .54 and .52 respectively.

According to FOURTAU, the apical system of *B. orientalis* is situated anteriorly to the centre (.44 of the length). In *B. somaliensis*, the apical system is central or very slightly to the posterior.

The apical surface of *B. orientalis* is more uniformly rounded than that of *B. somaliensis* which is usually bluntly conical, the apical disc being at the apex. This conical appearance of the apical surface in *B. somaliensis* is very marked in some specimens, but is only slight in others, which tend to have the more rounded appearance of *B. orientalis*. The margin of the test in *B. somaliensis* appears to be thinner and more undulating than that of *B. orientalis*.

\* FOURTAU, 1924. "Catal. des Invert. Foss. de l'Egypte, etc.," *Geol. Surv. Egypt*, Palæont. Ser. No. 6, Terr. Jurass., pt. 1, p. 27.



## EOCENE ECHINOIDEA.

## Family FIBULARIDÆ.

Genus SISMONDIA, Desor, 1858.

*Sismondia*, spp.*Material*.—A number of pieces of limestone containing specimens of *Sismondia*.*Localities*.—(1) Top of gypsum hill, Shahán, between Erigavo & Sehet, E. Som. (2) Hills to the east of Bihen-Gaha Pass, E. of Berbera, N. Som. (3)  $2\frac{1}{2}$  miles west of Gabile, in Ferrio Range, Central Som.

Of the specimens of *Sismondia* in the limestone, I have not, unfortunately, been able to remove even one completely from the matrix. There are at least two species represented, for there are apical surfaces with straight-sided narrow petals, and others, more numerous, with wider tapering petals. There are also oral surfaces with the periproct near the margin and oral surfaces with the periproct almost halfway between the margin and the peristome. One cannot with certainty correlate the apical and oral surfaces in the limestone, but it is probable that the specimens with tapering petals and those with the periproct halfway between margin and peristome represent one species; while the specimens with narrow petals and those with the periproct near the margin represent the other. The association of the oral and apical surfaces in the limestone, on the whole, supports this relationship. The specimens of limestone in which the apical surfaces have the wider type of petals are marked A and those with narrow petals B. As it is often difficult to distinguish the oral surfaces definitely as A or B, the labelling refers mainly to the apical surfaces. Some of the specimens of limestone from Locality 1 show apical surfaces of A and oral surfaces of both A and B. I considered the possibility of there being two species with wide tapering petals but was unable to detect two types of the wider petals.

*Sismondia*, sp. indet. (A).*Dimensions*.—The antero-posterior diameter varies from about 6 to 11 mm. The transverse diameter is about .9 of the antero-posterior diameter.*Localities*.—1 (B.M., E. 18030-33) and 2 (E. 18037).

*Description of the Species*.—Ambital outline subcircular to elliptical, sometimes slightly pentagonal. Apical surface probably comparatively high and uniformly rounded. Four genital pores. Ambulacral petals wide, their greatest breadth at about one-third of their length from their adoral extremity; from that point they taper gradually towards the apex and contract slightly adorally, having the appearance of a rounded adoral extremity although the pore-fields do not meet. Pore-fields widest at the widest part of the petal, and from there, contracting slightly adapically and adorally. Perradial tract widest at the mid-length of the petal, and from there contracting adapically and adorally. At the widest part of the petal the pore-fields and the perradial tract are usually about equal in breadth, although one may be rather more or less than the other. Pores small, conjugate, slightly elongated. Pairs of pores oblique, the conjugation lines becoming more oblique towards the adoral ends of the petals. In some specimens the pore-fields appear to be slightly depressed. Peristome pentagonal. Periproct sub-pentagonal?, its adoral margin about halfway between the margin and the peristome.

*Affinities*.—This species does not seem to agree with any of the known species of

*Sismondia*. It is similar to *S. logotheti* De Loriol \* from the Lower Eocene (Upper Libyan) of Egypt and to *S. polymorpha* Duncan and Sladen,† from the Kirthar Series of Sind in the position of the periproct and in having wide tapering petals, but differs from both in the form of the test and in the details of the petals. The apical surface of *S. logotheti* is conical and the test is thin on the margin and the pore-fields appear to be relatively narrower than in the present species. In *S. polymorpha*, the apical surface is almost flat, the pore-fields curve outwards at their adoral extremities and the perradial tract is very wide. In the form of the test, the present species is probably more like *S. scemanni*, De Loriol ‡ from the Middle and Upper Eocene of Egypt, but in that species the periproct is probably nearer the posterior margin and certainly the petals are different; their widest point is nearer their adapical than their adoral extremity and the perradial tract, compared with the breadth of the pore-fields, is much wider than in the present species.

*Sismondia*, sp. indet. (B).

The specimens of this species showing apical surfaces are few in number. The test is subcircular, in ambital outline with uniformly rounded apical surface. The diameter varies from about 3.5 mm. to probably as much as 7.5 mm. The periproct is situated near the margin, and on the margin in very small specimens. The petals, for the greater part of their length, have straight almost parallel pore-fields. In some specimens the pore-fields appear to continue thus to the adoral extremity of the petal, but in others again they appear to taper towards one another at that extremity. The perradial tract is equal to, or a little broader than, a pore-field. In some specimens the petals are raised above the level of the interambulacra. The pores are small, round, and conjugate, the conjugation lines horizontal. *S. isidis*, Fourtau § has similar round, conjugate pores in straight pore-fields, but in that species the petals are wider and the perradial tract wider than in the present species. Moreover, in *S. isidis*, the periproct is situated midway between the margin and the peristome.

*Localities*.—1 (B.M., E. 18034-36) ?, 2 (E. 18038), and ? 3 (18039).

Family NUCLEOLITIDÆ.

Genus PYGAULUS, Agassiz, 1847.

*Pygaulus*? sp.

*Material*.—Several specimens which are all more or less silicified and are very imperfectly preserved. The general form and longitudinally elongate peristome suggest the genus *Pygaulus* which, however, is typically Cretaceous.

*Dimensions*.—B.M., E. 18061, length, 20.5 mm.; breadth, 16.0 mm.; height, about 12.0 mm.

*Locality*.—Top of the Golis Range, W.S.W. of Upper Sheikh, N. Som.

\* DE LORIO, 1880. "Monogr. Echinides num. d'Egypte," *Mém. Soc. Phys. and Hist. Nat. Genève*, t. xxvii, p. 72, pl. ii, figs. 1-5.

† DUNCAN and SLADEN, 1884. "Descr. Foss. Echinoidea W. Sind," *Pal. Indica*, ser. xiv, vol. 1, 3, fasc. iii, p. 137, pl. xxv, figs. 1-13.

‡ DE LORIO, 1880. *Loc. cit.*, p. 73, pl. ii, figs. 6-7.

§ FOURTAU, 1909. "Descr. des Echinides Foss, etc.," *Mém. Instit. Egypt.*, t. vi, fasc. ii, p. 127, pl. vii, figs. 11-14.

## Family CASSIDULIDÆ.

Genus CASSIDULUS, Lamarek, 1801.

*Cassidulus?* sp.

*Material*.—One specimen, B.M., E. 18047, which is broken, silicified, and iron stained. The peristome is not visible, so that, as far as one can tell, the specimen might equally well be a *Nucleolites*. Its length is 19.4 mm.

*Locality*.—Hill at Dubbar Well, between Upper Sheikh and Burao, N. Som.

## Gen. and sp.?

*Material*.—Specimen B.M., E. 18067, a silicified test, stained with iron.

*Dimensions*.—Length, 24.6 mm.; breadth, 21.3 mm.; height, 14.8 mm.

*Locality*.—Top of the Golis Range, W.S.W. of Upper Sheikh.

*Description of Specimen*.—This specimen is elliptical in ambital outline, with apical and oral surfaces both flat and the margin of the test steep and rounded. The periproctal opening is greatly enlarged, occupying most of the posterior margin of the test, and its natural shape and position cannot be determined with certainty. The peristome is surrounded by a well developed floscelle, and had it been of the ordinary type, one would have said that the specimen was probably a *Catopygus*; but the floscelle appears to be unusual and suggests that the specimen may represent a new genus. On looking at the oral surface, one receives an impression that the bourrelets are radial in position and the phyllodes interradiar. Certainly in the radial position of the ambulacra there are prominences like bourrelets separated by hollows in the interambulacral areas. Each interambulacral hollow ends at the peristome in a very small knob or tubercle which, no doubt, corresponds to the real bourrelet. The specimen is very poorly preserved and no trace of the pores is apparent, but it is likely that they extended round the bases of the ambulacral prominences to the peristome.

## Gen. and sp. ?

*Material*.—A small specimen, B.M., E. 18075 (silicified and iron stained).

*Dimensions*.—Length, 15.5 mm.; breadth, 13.2 mm.; height, 9.8? mm.

*Locality*.—East side of Bosti, about twelve miles S.S.E. of Berbera, N. Som.

*Description of the Specimen*.—This specimen is oval in ambital outline, its greatest breadth about one-third of its length from the posterior; from there it contracts towards a rounded anterior end and more rapidly to the posterior, which is sub-rostrate. Oral surface flat, apical surface high and rounded, the highest point posteriorly eccentric. Periproct low down and not visible from above; it is broken, but it appears to be marginal or infra-marginal, set obliquely at the extremity of the posterior rostration, by which it is slightly overhung. Only a small portion of an ambulacral petal is exposed, and in it the pores are small and round. The peristome, which is slightly to the anterior of the centre, is elliptical, elongated in the direction of the antero-posterior axis, and surrounded by an ornamental rim. Unfortunately one cannot make out the detail of this structure.

*Affinities*.—This specimen seems to agree in most respects with the genus *Neocatopygus* described by DUNCAN and SLADEN \* from the Ranikot Series of Sind. Its main difference from that genus is in the peristome being elliptical, whereas that of *Neocatopygus* is pen-

\* DUNCAN and SLADEN, 1882. "Foss. Echinoidea W. Sind, etc.," *Pal. Ind.*, ser. xiv, fasc. ii, p. 76.



tagonal; both are surrounded by an ornamented wall-like rim. The periproct of *Neocatopygus* is described (*loc. cit.*) as supra-marginal, but in the figures given of the genotype, *N. rotundus* (*op. cit.*, pl. xvi), it appears to be obliquely marginal, low down on the test and not visible from above. The periproct of the present specimen, when complete, may quite well have been similar to that of the figured *Neocatopygus*.

Genus ECHINOLAMPAS, Gray, 1825.

*Echinolampas* cf. *amygdala*, Desor.

- Echinolampas amygdala*, Desor, 1847. In Ag. and Desor. Catal. Rais. des Echinides, *Ann. Sci. Nat.*, ser. 3, t. 7, p. 164.  
 „ „ Desor, 1857. *Synopsis des Echinides Foss.*, p. 304.  
 „ „ De Loriol, 1880. Monogr. des Echinides Num. d'Egypte, *Mém. Soc. Phys. and Hist. Nat. Genève*, t. xxvii, p. 96, pl. vi, figs. 2-3.  
 „ „ Cotteau, 1891. *Pal. Franc.*, Terr. Eoc., ii, Echinides, p. 159.  
 „ „ (pars) Fourtau, 1898. "Revis. des Echinides," *Mém. Institut Egypt.*, t. iii, fasc. viii, p. 660.  
*Echinolampas perrieri*, Gregory non De Loriol, 1898. Egypt. Echinoidea, *Geol. Mag.*, dec. iv, v, p. 156.  
*Echinolampas amygdala*, Fourtau, 1913. Catal. Invert. Foss. de l'Egypte, *Geol. Surv. Egypt*, Palæont. Ser. No. 1, Terr. Tert., pt. i, Echinides Eoc., p. 32.

*Material*.—Three specimens, one of which, B.M., E. 18058, may be regarded as typical of the species. It is well preserved, except that a part of the oral surface, including the peristome, is broken. B.M., E. 18059 is crushed, but it shows the peristome very well.

*Dimensions*.—B.M., E. 18058; length (L), 45.5 mm.; breadth (B), 37.6 mm.; B/L, .82; height (H), 22.5 mm.; H/L, .49.

*E. amyg.* De Loriol; length (L), 30-38 mm.; B/L, .74; H/L, .50.

*E. amyg.* Coll. Egypt. Surv.; length (L), 46 mm.; breadth (B), 38 mm.; B/L, .83; height (H), 20.5 mm.; H/L, .44.

*Localities*.—Endasaf Hill (Asseh Hills), E. of Dodab and S. of Raguda, E. Som. A little S. of Bokh Camp and Durdur, E. Som.

B.M., E. 18058 is very like the specimens of *E. amygdala*, Desor, from the Mokattam of Egypt figured by DE LORIOLO (*loc. cit.*), one of which, according to DE LORIOLO, is the type-specimen. The dimensions of the Somaliland specimen (E. 18058) are not in complete agreement with those given by DE LORIOLO for the species, the breadth in E. 18058 being .82 of the length and therefore greater than in DE LORIOLO's specimens. (See dimensions above.) In its greater breadth it is nearer the specimen in the collection of the Geological Survey of Egypt, referred by Dr GREGORY in 1898 (*loc. cit.*) to *E. perrieri*, and later by the late R. FOURTAU (*loc. cit.*, 1913) to *E. amygdala*. This specimen differs further from DE LORIOLO's specimens in its height being only .44 of its length.

Details as to the number of pore-pairs in the petals of *E. amygdala* are not available, so comparison on this point must be omitted. It may be of use to give these details of E. 18058.

In Amb. III the right pore-field (*i.e.* column *a*) has three pore-pairs more than the left (or column *b*).

In Amb. IV the posterior pore-field has about thirty-eight pairs of pores, having about ten pairs more than the anterior pore-field.

In Amb. I the anterior pore-field has about forty-two pairs of pores, having seven pairs more than the posterior pore-field.

Apart from the difference in dimensions the only other apparent point in which the Somaliland specimens differ from the specimens figured by DE LORIOI is in the position of the apical system. In E. 18058 the apical disc is situated about .43 of the length from the anterior vertical plane. According to DE LORIOI, the apical disc in *E. amygdala* is "très excentrique en avant," and in the figures (*loc. cit.*) it is certainly farther to the anterior than .43 of the length. It is possible that with variation in the dimensions there is also some slight variation in the position of the apical disc. Without seeing specimens of the rare *E. amygdala*, one can only refer the Somaliland specimens provisionally to that species, with which they may be identical and which they at least very strongly resemble.

Genus PLESIOLAMPAS, Duncan and Sladen, 1882.

*Plesiolampas* ? n. sp.

*Material*.—One poorly preserved silicified specimen, B.M., E. 18060.

*Dimensions*.—Length, 28.3 mm.; breadth, 23.3 mm.; height, 11.8 mm.

*Locality*.—Top of the Golis Range, W.S.W. of Upper Sheikh.

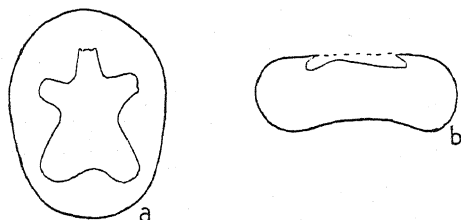


FIG. 6.—*Plesiolampas*, n. sp.

FIG. 6a.—Outline of apical surface of B.M., E. 18060

FIG. 6b.—Profile outline of same.

This specimen is probably a *Plesiolampas* allied to those from the Ranikot Series of Sind described by DUNCAN and SLADEN (1882, *loc. cit.*, pp. 54–61). The form of the test is striking and the species would doubtless be easily recognisable. It is oval in ambital outline, its greatest breadth about one-third of its length from the anterior margin. The apical surface, now broken, was no doubt flat. The oral surface is concave, being

strongly arched in the direction of the antero-posterior axis and only slightly transversely. The margin of the test is tumid, especially anteriorly.

Family SPATANGIDÆ.

Genus PERICOSMUS GREGORYI, n. sp.

*Diagnosis*.—A *Pericosmus* of depressed form; subcircular in ambital outline; apical and oral surfaces almost flat, only slightly rounded, margin of the test steep and rounded, ambitus about the middle height. Anterior groove hardly appreciable. Apical system ethmolysian with two genital pores. Ambulacral petals only slightly sunken, the pore-fields about twice the breadth of the perradial tract.

*Material*.—Holotype: (B.M., E. 18080). The specimen is silicified and iron stained.

*Dimensions*.—Length, 54.8 mm.; breadth, 55.6 mm.; height, 35? mm.

*Locality*.—1½ miles from Mukroh Camp, S. of Hais, E. Som.

*Description of the Specimen*.—The specimen is subcircular in ambital outline with a very slight anterior indentation. The apical surface of the test is almost flat, being only slightly rounded, and the oral surface, which is almost entirely removed, was probably gently rounded also. Margins of the test steep and rounded, the ambitus about the middle height. The apical system, which is central, is ethmolysian with two genital pores. The ambulacral petals are long, straight, narrow, only slightly depressed and very divergent, the anterior pair being longer than the posterior pair by about one-quarter of their length. The pores are

elongated, the exterior longer than the interior one and tapering towards it, and each pore-field is almost twice the breadth of the perradial tract. Three small portions of a fasciole are apparent, two of them quite distinct, and the third so faint as to be doubtful. The most apparent portion occurs just below the ambitus in Amb. II. Another small portion occurs about the level of the ambitus in interambulacrum 3. The doubtful portion referred to occurs at a much lower level in interradius 1, and, if authentic, it would indicate that the fasciole is a marginal one and passes below the periproct.

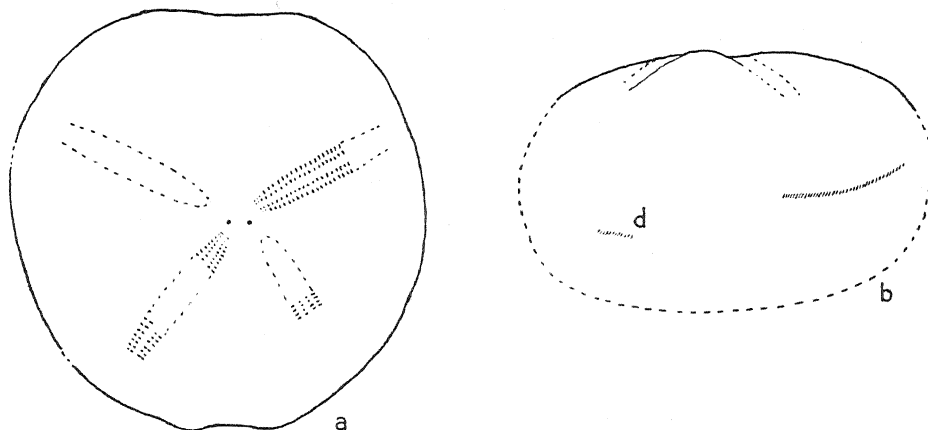


FIG. 7.—*Pericosmus gregoryi*, n. sp.

FIG. 7a.—Diagram of apical surface of the holotype, B.M., E. 18080.

FIG. 7b.—Diagram of profile of same, "d" doubtful portion of fasciole.

*Affinities.*—Comparison of specimen E. 18080 with various genera of the *Spatangidae* suggested five as possible, viz. *Iraniaster*, *Lambertiaster*, *Holcopneustes*, *Prenaster*, and *Pericosmus*. *Lambertiaster*, Gauthier\* and *Iraniaster*, Cotteau and Gauthier,† are Upper Cretaceous genera which agree with the Eocene *Holcopneustes*, COTTEAU,‡ in having a peripetalous fasciole, the course of which extends some distance from the extremities of the ambulacral petals and which is sometimes marginal anteriorly. As there is no trace of an ordinary peripetalous fasciole in E. 18080, it seemed possible that the fasciole might be of this type. *Iraniaster* and *Lambertiaster* differ from *Holcopneustes* in their sub-pentagonal peristomes and from one another in the type of their sterna. As the oral surface of E. 18080 is quite destroyed, identification with any one of these three genera would be extremely doubtful. It is sufficient in this case, however, to note that while in all three the peripetalous fasciole is some distance from the extremities of the petals and is sometimes marginal anteriorly, it is never so far distant from the extremities of the petals as in the present specimen, which leads one to consider its fasciole as more probably marginal than distantly peripetalous. The doubtful fragment of a fasciole near the posterior, already referred to, tends to confirm one in this opinion.

*Pericosmus*, Agassiz,§ and *Prenaster*, Desor,|| remain to be considered. Both have marginal fascioles and *Pericosmus* has also a peripetalous fasciole, while *Prenaster* has a posterior peripetalous fasciole which joins the marginal one laterally. As already stated, no trace of a peripetalous fasciole is apparent in E. 18080, but, as it resembles *Pericosmus*

\* GAUTHIER, 1892. *Notes sur les Echinides Cret. rec. en Tunisie*, par M. Aubert, p. 28, pl. iii.

† COTTEAU and GAUTHIER, 1895. In DE MORGAN, *Miss. Sci. en Perse*, iii, pt. 2, p. 26.

‡ COTTEAU, 1889. "Echinides rec. dans la Prov. d'Aragon," *Ann. Sci. Nat. Zool.*, (7) viii, p. 34, pl. iii, figs. 20-22.

§ AGASSIZ, 1847. "Catal. Rais.," *Ann. Sci. Nat.*, ser. 3, vol. viii, p. 19.

|| DESOR, 1853. "Note sur les Ech.," *Act. Soc. Helv. Sci. Nat.*, p. 279.



rather than *Prenaster*, I have assigned it to that genus. In *Prenaster*, the test is usually more tumid and the apical disc is always very eccentric to the anterior. There is no apparent reason why the present specimen should not be a *Pericosmus* except the absence of a peripetalous fasciole. Usually in this genus the peripetalous fasciole is apparent although the marginal one may be doubtful.

The present specimen, in its depressed, suborbicular form, differs from most species of *Pericosmus*. Its apical and oral surfaces are almost flat and its ambitus is about the mid-height; whereas in most specimens of the genus the oral surface is comparatively flat, the apical surface high, and the ambitus near the base-plane. As a rule the anterior indentation is more marked than in the present specimen. E. 18080 is most like *Pericosmus bastennesensis*, Cotteau,\* from the M. Eocene of France, but its apical surface is more depressed and its ambulacral petals are longer and narrower than those of the French species.

Genus, LINTHIA, Mérian, 1853.

*Linthia somaliensis*, n. sp.

*Diagnosis*.—Test depressed, ruggedly oval in marginal outline, contracted slightly towards the posterior to an indefinite posterior truncation; deeply indented by the anterior sulcus. Posterior face almost vertical. Posterior interambulacrum subcarinate on the apical surface, inflated on the oral surface. The pore-pairs in Amb. III on the apical surface, in depressions in the adoral, adradial corners of the plates. The amb. petals in rounded, comparatively shallow grooves and of almost uniform breadth except where they taper at the apical disc. The pores large, circular, conjugate, those of a pair separated by a distance slightly greater than their own diameter. Perradial tract in the petals very narrow in comparison with the breadth of the pore-fields, approximately one-half. The pore-pairs situated in well-defined grooves separated by ridges bearing granules or small nodosities.

*Material*.—Holotype: Brit. Mus., E. 18051. Paratypes: Brit. Mus., E. 18052–54 and E. 18079. The holotype is complete except at the periproct, but the apical system and the greater part of the ambulacral petals are obscured by matrix. Its surface is abraded. E. 18052 is a broken and weathered specimen, but it shows the apical system, the peristome, and part of the petals. E. 18053 shows one posterior petal completely. E. 18079 is a young individual, the test of which is broken both at the anterior and at the posterior. The sutures of the plates are all developed by weathering.

*Dimensions*.—Holotype, B.M., E. 18051: length (L), 36.0 mm.; breadth (B), 34.0 mm.; B/L, .94; height (H), 21.4 mm.; H/L, .59.

B.M., E. 18079: length (L), 31? mm.; breadth (B), 28.2 mm.; B/L, .9; height (H), 19.4 mm.; H/L, .62.

*Localities*.—South of Bokh Camp and Durdur, E. Som. Gelidi, between Tosdai and Mugeh Tug, E. Som.

*Description of the Species*.—Ambital outline ruggedly oval, indented by the anterior sulcus to a depth of about 2 mm. in the holotype; slightly contracted towards the posterior to an ill-defined posterior face. The anterior sulcus is fairly wide and deep adapically; it becomes narrower and deeper at the ambitus and is continuous to the peristome, although much reduced in both depth and breadth on the inferior surface. Greatest breadth of the test in line with the apical system which in the holotype is probably about .4 of the length

\* COTTEAU, 1887. *Pal. Franc.*, Terr. Tert., i, Echinides Eoc., p. 432, pl. 119.

from the anterior vertical plane. Highest point of the test on the subcarinate posterior interradius, about one-third of the length from the posterior vertical plane in the holotype. Ambitus in the holotype, about one-third of the height above the base-plane. The plastron is strongly inflated, especially to the posterior, where it culminates in a prominent nodosity. Only the plastron rests on the base-plane. The holotype and E. 18054 are not perfectly symmetrical, the right anterior interambulacrum projecting slightly forward beyond the left. This asymmetry is not striking, but became apparent when one measured the holotype.

Apical System.—Exposed in E. 18052 in which the genital pores are much enlarged and the sutures developed by weathering. Ethmolysian with four large circular gonopores, the anterior pair smaller and closer together than the posterior pair. Genital 1 is contiguous with 2, and 3 with 4, thus pushing outwards oculars II and IV; genitals 2 and 3 are very little in contact and are almost separated by ocular III. Genital 2 is produced to the posterior in a madreporite separating oculars I and V.

Ambulacra.—The adapical plates in Amb. III are broad and low, becoming higher adorally. Although the pores are not distinct in any of the specimens, they are evidently situated in depressions in the adoral adradial corners of the plates. Amb. III is not completely visible in any of the specimens.

The amb. petals which lie in rounded grooves are of almost uniform breadth, contracting slightly at their adoral extremity and tapering rapidly at the apical disc. The anterior petals are slightly longer than the posterior pair.

	Length of petal.		No. of pore-pairs.		Greatest breadth of petal.	
	p.p.	a.p.	p.p.	a.p.	p.p.	a.p.
B.M., E. 18051	..	..	..	..	4.0 mm.	
B.M., E. 18079	10 mm.	13.5 mm.	15 or 16	17 or 18	3.5 mm.	4.0 mm.
B.M., E. 18052	12.5 mm.	..	15	17 or 18	4.5 mm.	5.0 mm.
B.M., E. 18053	12.0 mm.	..	14 or 15	..	4.5 mm.	

The petals (post. and ant.) are not perfectly symmetrical, but have a very slight sigmoid curvature. The pore-fields are wide in comparison with the breadth of the perradial tract. The pore-fields of the posterior petals at their mid-lengths are about twice the breadth of the perradial tract in the holotype. They are rather more than twice in E. 18053 and less than twice in E. 18079. From that point both the pore-fields and the perradial tract contract slightly adorally; adapically, the pore-fields contract while the perradial tract becomes rather wider.

The anterior petals of the adult individual are not known, as E. 18079 is the only specimen in which an entire anterior petal is visible. This specimen, which is a younger individual, is smaller and more rotund in form than the other specimens, and its ambulacra are less sunken and its interambulacra less tumid. At the mid-length of its anterior petals the perradial tract is about two-thirds of the breadth of a pore-field. From that point the perradial tract and the pore-fields contract slightly towards their adoral extremity, and towards the apex of the area the pore-fields contract and the perradial tract becomes wider. The anterior petals in E. 18052 are incomplete, but they probably differ from those of E. 18079 only in being more deeply sunken. In E. 18054 the anterior pore-field of one of the anterior petals is preserved, and it appears to be less uniform in breadth than those of E. 18079 and E. 18052. It is

very wide at a point about one-third of its length from the adoral extremity and from there contracts towards the apex.

The pore-pairs of the posterior and anterior petals are similar, differing only in those of the posterior petals being more closely set together. The pores are large and circular, those of a pair separated by a distance slightly greater than their own diameter. Each pair of pores is situated in a groove adjacent to the adoral margin of an amb. plate. Adjacent to the adapical margins of the plates and separating the grooves containing the pore-pairs are ridges, each bearing a row of irregular, indistinct granules, or they may be composed of small nodosities. In some specimens (E. 18051, E. 18053, E. 18079) the ridges which extend from the adradial suture towards the perradial die away before reaching the perradial suture, and thus is produced a smooth perradial tract. In E. 18052 the ridges, where visible, are continuous to the perradial suture, and the perradial tract bears a zig-zag arrangement of small nodosities formed by the end of the ridges. It may be that the smooth perradial tract is the result of weathering of the surface of the test. The amb. pores near the peristome are in deep pits.

Interambulacra.—The interambulacra on the apical surface are prominent and rounded. The plates are slightly curved so that their sutures are slightly depressed, this being most marked in the interradian suture. This plate curvature is not so apparent in the young individual E. 18079. On the oral surface the holotype exhibits normal heteronomy in inter-radius 1 (*i.e.* fusion of 2a and 3a). Plate 2a just fails to touch plate 1, so that plate 2b has a slight contact with amb. 1. In interradius 5 the labrum is succeeded by two large sternals which swell up to a nodosity at their posterior end.

Peristome.—Opening sub-pentagonal to crescent-shaped. The labrum projects over the opening and is bounded along its margin by a narrow, raised rim. In E. 18052 the labrum is about 1.5 or 2 mm. above the anterior margin of the peristome. In the same specimen, which is much worn, the transverse diameter of the peristome is 6 mm. and the sagittal diameter 2 mm. In E. 18079 the transverse diameter is 4.5 mm.

Periproct.—Not complete in any of the specimens. Probably vertically elongate. The almost vertical posterior face at the upper end of which it is situated is slightly depressed below the periproct.

Ornament.—The specimens are all much worn, so that the tuberculation is not distinct. The primary tubercles are largest on the actinal surface near the peristome, where they are situated on small, raised scrobicules (some oblique?) surrounded by a ring of miliaries.

A peripetalous fasciole and a lateral one is apparent in the holotype and part of the peripetalous one in E. 18054. In the holotype the peripetalous fasciole crosses the anterior sulcus a short distance above the ambitus, and its course from there to the extremities of the petals II and IV has a slight convexity directed adapically. It forms obtuse angles at the ends of petals II and IV and then turns sharply adapically in interambulacra 1 and 4. It continues thus for a short distance only, when it makes re-entering angles and curves to the extremities of petals I and V. It crosses the posterior interradius in an almost straight course at a point about 13 mm. from the position of the apical system in the holotype. The lateral fasciole leaves the peripetalous one where it turns sharply into interambulacra 1 and 4.

*Affinities.*—Although I have assigned this species to the genus *Linthia*, I only do so provisionally. Dr F. A. BATHER\* would doubtless regard it as *Hemiaster* on account of the normal heteronomy of interradius 1 on the oral surface. For this reason, he assigned his species *sudanensis* from Sokoto to *Hemiaster*, although in other respects it approached

\* BATHER, 1904. "Eocene Echinoids from Sokoto," *Geol. Mag.*, dec. v, i, p. 297.



more nearly certain species of *Linthia*. According to LOVEN,\* *Desoria*, which is synonymous with *Linthia*, has ancient heteronomy, and, according to P. M. DUNCAN,† *Linthia* has ancient heteronomy. Dr BATHER, following these authorities, assumed the heteronomy in *Linthia* to be of ancient type and that in *Hemiasler* of normal type. Although I have no definite evidence to the contrary, I am yet doubtful as to whether a typical *Linthia* has really ancient heteronomy. It seems probable that a number of species known as *Linthia* may have heteronomy of normal type and such may quite well be the case in the type-species, *L. insignis*, Mérian. Dr BATHER recommended the examination of the genotype on this point in 1904 (*loc. cit.*), but so far as I know this has not been done. I also have not so far been able to settle the point.

Professor GREGORY has been extremely kind in endeavouring to obtain a specimen of *L. insignis*. At the request of Professor GREGORY, Professor SCHARDT of Zurich, although unable to supply *L. insignis*, kindly sent a specimen of *L. subglobosa*, Lamarck, which he has, since then, kindly presented to the Hunterian Museum. This specimen is not well preserved, but one was able to expose a suture-line on the oral surface in interradius 1, the position of which leads one to believe that heteronomy of normal type is most probably present. The same may be said of the specimen I have referred to on p. 436 as *Linthia aff. insignis*.

The present species *somaliensis* agrees with the species *sudanensis*, Bather, in having normal heteronomy in interradius 1, but resembling species of *Linthia* rather than *Hemiasler*. It seems to resemble most the species *L. cavernosa*, De Loriol (syn. *L. aschersoni*, De Loriol) from the Lower Eocene of Egypt, and, through the kindness of the Keeper of the Geological Department of the British Museum, Dr F. A. BATHER, I have been able to examine specimens of these species belonging to the British Museum. Normal heteronomy in interradius 1 is apparent in the specimen of *L. cavernosa*, Brit. Mus., E. 11435, and indications of it in E. 11436 and E. 11437. Normal heteronomy is also apparent in the specimens E. 11442 and E. 11443, labelled *L. aschersoni*, De Loriol.

The question of the type of heteronomy in *Linthia* can only be settled by examination of the genotype, but it is suggestive that in the only species of so-called *Linthia* examined on this point there are at least indications that the heteronomy is of normal type. The species are *sudanensis*, *cavernosa* (syn. *aschersoni*), *somaliensis*, *subglobosa*, and *aff. insignis*. The number is small and proves nothing, but until the genotype is examined it is at least less confusing to call them *Linthia*, especially as they have lateral as well as peripetalous fascioles.

As already stated, *L. somaliensis* is very similar to *L. cavernosa*, De Loriol ‡ from the Lower Eocene of Egypt, with which, according to R. FOURTAU,§ *L. aschersoni*, De Loriol || is synonymous. *L. cavernosa* is relatively broader than *L. somaliensis*, and it is usually higher although it varies to lower. In the ambulacral petals the pore-pairs are smaller and more closely set than in *somaliensis*, and it has a greater number of pairs for the size of the individual; the perradial tract is equal to, or greater than, the breadth of a pore-field, whereas in *L. somaliensis* the perradial tract is always much narrower than a pore-field.

*Linthia esnehenis*, De Loriol,¶ is near to *L. cavernosa* and differs from *L. somaliensis* in the same respects and also in the pores of Amb. III being level with the test instead of being in depressions in the plates as in *somaliensis*.

\* LOVÉN, 1874. "Etudes sur les Echinoïdées," *Kongl. Svenska, Vet.- Akad. Handl.* (n.s.) xi, No. 7, p. 52.

† DUNCAN, 1889. "Revis. of Gen., etc., of the Echinoidea," *Journ. Linn. Soc., Zool.*, 1891, xxiii, p. 233.

‡ DE LORIOI, 1880. *Loc. cit.*, p. 55, pl. viii, figs. 8-10.

§ FOURTAU, 1913. *Catal. Invert. Foss. de l'Egypte, Geol. Surv. Egypt, Palæont. Ser. No. 1, Terr. Tert., pt. i, Echinides Eocene*, p. 51.

|| DE LORIOI, 1881. *Loc. cit.*, p. 37, pl. ix, figs. 1-4.

¶ DE LORIOI, 1881. *Loc. cit.*, p. 39, pl. ix, figs. 5-6.

*Linthia* sp. aff. *insignis*, Mérian.

*Linthia insignis*, Mérian, in Desor, 1853. "Notice sur les Echinides," *Acta soc. sci. nat.*, 38<sup>e</sup> session, Porrentruy.

(Not seen.)

" " Desor, 1857, *Syn. Echinides Foss.*, p. 395, pl. xliii, fig. 9.

" " De Loriol, 1875. "Descr. Echinides Foss. de la Suisse," *Mém. Soc. Pal. Suisse*, vol. ii, pt. iii, p. 101, pl. xv, fig. 1, pl. xvi, figs. 1-2.

" " Cotteau, 1886. *Pal. Franc.*, Terr. Tert., Echinides Eoc., i, p. 232, pl. 70.

**Material.**—One large specimen, B.M., E. 18055. It is broken on one side, the ambulacral petals are entirely concealed by matrix and the surface of the test is much abraded. A number of very small spines are embedded in matrix on the plastron.

**Dimensions.**—Length (L), 83.7 mm.; breadth (B), .74 mm. ?; B/L, .88; height (H), 58.5 mm.; H/L, .7.

**Locality.**—A little S. of Bokh Camp and Durdur.

**Affinities.**—This specimen resembles those large species of *Linthia*, *L. insignis*, Mérian, and *L. rousseli*, Cotteau, its relatively great height and somewhat conical upper surface rendering its resemblance to the former the more striking. As it is not sufficiently well preserved to enable one to describe it fully, it will suffice to note its apparent points of difference from those species it resembles.

It differs from *L. insignis* from the Eocene of Switzerland and France (M. Eocene: rare) in several points. The posterior face in the Somaliland *Linthia* is almost vertical, whereas that of *L. insignis* is obliquely downwards and inwards; although in connection with this point it is of interest to note that DE LORIOI figured a small specimen of *L. insignis* (*loc. cit.*, pl. xvii, fig. 2) in which the posterior face is almost vertical. The undercut posterior extremity of the test of *L. insignis* tends to render the ambital outline acuminate at the posterior, whereas in the Somaliland *Linthia*, the posterior outline of the test is straight for about  $2\frac{1}{2}$ –3 cm., the breadth of the vertical truncation. In its great height, .7 of the length, the Somaliland *Linthia* resembles the more tumid specimens of *L. insignis* described by DE LORIOI (*loc. cit.*), who recorded variation in the height from .53 to .79 of the length. Specimen E. 18055 is broken on one side, but one would estimate its breadth as about .88 of the length. It is therefore narrower than *L. insignis* in which, according to DE LORIOI, the breadth varies from .94 to 1.00 of the length, and in the French specimen figured by COTTEAU (*loc. cit.*) the breadth is greater than the length. The apical system of the Somaliland *Linthia* is probably less anterior in position than that of *L. insignis*, and its peripetalous fasciole is less sharply angular at the extremities of the petals and does not run so far adapically in the interambulacral areas. Only a small portion of the lateral fasciole is preserved.

*Linthia rousseli*, Cotteau,\* from the M. Eocene of France, agrees with the Somaliland specimen in its almost vertical posterior face, but in *L. rousseli* the height of the test is less (.58 of the length), and the upper surface is not conical but uniformly rounded. Furthermore, the inferior surface is flatter than that of the Somaliland specimen and the course of the fasciole is different.

On a previous page (p. 435) there is some discussion regarding the type of heteronomy in interradius 1 characteristic of the genus *Linthia*, and in this connection I desired very much to know the type of heteronomy in interradius 1 in the present specimen. Its surface, as already stated, is much abraded, the tubercles being worn down almost to a level of the coating of the matrix. I considered that further abrasion of interradius 1 at the peristome

\* COTTEAU, 1886. *Pal. Franc.*, Terr. Tert., i, Echinides Eoc., p. 235, pls. 71 and 72.

could detract little from the specimen and might be of some use. I therefore took the liberty of "weathering" a part of interambulacrum 1 until a suture line became apparent. This suture is no doubt part of the median suture, and its position seems to indicate that the heteronomy is of normal type.

*Linthia* ? n. sp.

Syn. *Hemiaster*, sp. indet. Currie, 1925. *Monogr. Hunt. Mus.* i, 1925, p. 74, pl. ix, figs. 7 a-b.

*Material*.—B.M., E. 18056 and B.M., E. 18077, and probably also B.M., E. 18072 and B.M., E. 18073. The specimens are all more or less silicified and iron stained.

*Localities*.—Camp at head of Mah Tug near Ertoleh, E. Som. East side of Bosti. Top of the Golis Range, W.S.W. of Upper Sheikh.

The anteriorly situated apical system ( $\cdot 39$  of the length in the specimen E. 579 in the Hunterian Museum (*loc. cit.*)) suggests that this species is more probably *Linthia* than *Hemiaster*. The markedly anterior apical system, the almost level apical surface of the test and the deep and steeply sloping anterior ambulacral petals make the species a well-defined one.

Genus SCHIZASTER, Agassiz, 1847.

*Schizaster* ? sp. aff. *concinus*, Péron and Gauthier.

*Schizaster concinns*, Pér. and Gauth., 1885. In Cott. Pér. and Gauth., *Echinides Foss. de l'Algérie*, Etage Eocène, p. 60, pl. iv, figs. 2-3.

" " Cotteau, 1887. *Pal. Franc.*, Terr. Tert., Echinides Eoc., i, p. 357, pl. 107, figs. 7-9.

*Material*.—B.M., E. 18070, a flint cast stained with iron.

*Dimensions*.—Length (L), 40.5 mm.; breadth (B), 34.8 mm.; B/L,  $\cdot 86$ ; height (H), 25.8 mm.; H/L,  $\cdot 64$ .

*Locality*.—Top of the Golis Range, W.S.W. of Upper Sheikh.

This specimen shows some resemblance in its general form and the character of its ambulacral petals to *Schizaster concinns*, P. and G. from the Eocene of Algeria and France, and it is mainly for this reason that I have assigned it to the genus *Schizaster*, for its apical system is anterior to the centre ( $\cdot 42$  of the length from the anterior vertical plane), and the specimen could almost equally well be a *Linthia*. *S. concinns*, in which the apical disc is central, is also a border-line species, having some of the characters of *Schizaster* and some of those of *Linthia*, and PÉRON and GAUTHIER (*loc. cit.*) had to consider to which of these genera it could be most satisfactorily assigned. COTTEAU also discussed the point (*loc. cit.*). The present specimen differs from *S. concinns*, in addition to its more anteriorly situated apical disc, in being relatively narrower and in the anterior sulcus being deeper at the ambitus.

*Schizaster* ? cf. *symmetricus*, Duncan and Sladen.

*Schizaster symmetricus*, D. and S., 1884. *Foss. Echinoidea W. Sind*, *Pal. Indica*, ser. xiv, vol. i, 3, fasc. iii, p. 220, pl. xxxvii, figs. 15-21.

*Material*.—One crushed and broken specimen, B.M., E. 18057. Its length is about 28 mm.

*Locality*.—Endasaf Hill (Asseh Hills), E. of Dodab and S. of Raguda, E. Som.

*Affinities*.—This specimen is probably a *Schizaster*, and among species of that genus it appears to resemble most *S. symmetricus*, D. and S., from the Kirthar series of Sind. The test has suffered lateral compression, but its form was no doubt very similar to that of the



Sind species with its wide anterior sulcus and divergent anterior petals. The similarity in the character of the ambulacral petals is notable. They are very wide, the pores are slit-like (although now widened by weathering in the present specimen), those of a pair very far apart and the perradial tract much narrower than the pore-fields. The condition of the specimen does not allow of more detailed comparison.

*Schizaster deserti*, FOURTAU,\* from the M. Eocene of Egypt, appears to be another somewhat similar species from which the Somaliland specimen differs in the details of the ambulacral petals. The pores in the present specimen are more elongated, those of a pair are farther apart and the perradial tract is relatively narrower than in *S. deserti*.

*Schizaster cf. gaudryi*, De Lorient.

*Schizaster gaudryi* De Lorient, 1880. Monogr. Echinides Num. d'Egypte, p. 64, pl. ix, fig. 1.

**Material.**—Two incomplete and poorly preserved (silicified and iron stained) specimens, B.M., E. 18078 and B.M., E. 18074, may be referable to the above species from the Lower Eocene of Egypt.

**Localities.**—East side of Bosti. Top of the Golis Range, W.S.W. of Upper Sheikh.

*Schizaster?* sp. aff. *ournoueri*, Cotteau.

*Schizaster ournoueri*, Cotteau, 1887. *Pal. Franc.*, Terr. Tert., Echinides Eoc., i, p. 301, pl. 91, figs. 1-3.

**Material.**—Specimen B.M., E 18050, a flint cast encrusted with beekite and stained with iron oxide. In its general form and the appearance of the ambulacral petals it appears to be somewhat similar to *S. ournoueri*, Cotteau, from the M. Eocene of France.

**Dimensions.**—Length, 34.3 mm.; breadth, 32.1 mm.; height, 20.4 mm.

**Locality.**—Duro Hills near Dodab, E. of El Dur Elan, E. Som.

*Schizaster* ? sp. aff. *pyrenaicus*, Cotteau.

*Schizaster pyrenaicus*. Noticed in Jacquot and M.-Chalmas, 1886. "Exist. de l'Eocene inf. dans la Chalosse, etc.," *Compte rendu des séances de l'Acad. des Sciences*, p. 1263.

" " Cotteau, 1887. *Pal. Franc.*, Terr. Tert., Echin. Eoc., i, p. 291, pl. 88, figs. 1-5.

**Material.**—Specimen B.M., E. 18049, a flint cast encrusted with beekite and stained with iron oxide. Its general appearance recalls the species *S. pyrenaicus*, M.-Chalmas, from the Lower Eocene of France.

**Dimensions.**—Length, 37.0 mm.; breadth, 31.3 mm.; height, ?.

**Locality.**—Duro Hills near Dodab.

Genus *Opissaster*, Pomel, 1883.

*Opissaster farquharsoni*, n. sp.

**Diagnosis.**—An *Opissaster* with four genital pores and an anteriorly situated apical system. Test cordate in ambital outline with deep anterior indentation. The posterior face slightly oblique, sloping upwards and inwards. Amb. petals narrow, deeply sunken, the posterior pair slightly arched towards one another and the anterior pair slightly flexuous and very divergent. The grooves in which the petals lie with steeply sloping sides which

\* FOURTAU, 1909. "Descr. des Echinides Foss., etc.," *Mém. Instit. Egypt.*, t. vi, fasc. 2, p. 150, pl. viii, figs. 17-19.

die away towards the adoral extremities of the petals. The floor of the groove of almost uniform breadth and coinciding with the perradial tract, the pore-fields extending along the sloping faces of the grooves. The pores in both posterior and anterior petals circular, and those of a pair separated by a distance equal to their own diameter. Perradial tract and pore-fields approximately of equal breadth.

*Material*.—Holotype: Brit. Mus., E. 18048.

*Dimensions*.—Length (L), 42.2 mm.; breadth (B), 42.0 mm.; B/L, .99; height (H), 27.5 mm.; H/L, .65.

*Locality*.—Hobal Reren Hill, near El Dur Elan, E. Som.

*Description of Holotype*.—Test cordate in ambital contour with length and breadth almost equal. Ambitus about one-third of the height above the base-plane. Greatest breadth in line with the apical disc, which is situated about .4 of the length from the anterior vertical plane. Anterior sulcus broad and deep on the apical surface, becoming narrower but deeper where it indents the ambitus to a depth of about 3 mm., continuous to the peristome; but greatly reduced in depth and breadth on the inferior surface. Highest point of the test on the posterior interradius about .38 of the length from the posterior vertical plane. Observed in longitudinal profile the test slopes gently to the anterior until it joins the steeply rounded slope of the tumid anterior margin; towards the posterior the profile outline curves gently down to meet the line of the slightly oblique posterior face which slopes inwards and upwards. The test is broken in this region, only a part of the periproct and the posterior face being preserved. On the oral surface the plastron is prominent and rounded and only a small part of it rests on the base-plane. The specimen is slightly asymmetrical, the right anterior interradius projecting slightly farther forward than the left.

*Apical System*.—Ethmolysian with four genital pores. The sutures of the plates are not clear. The genital pores are large and circular, the posterior pair slightly larger than the anterior pair and set farther apart.

*Ambulacra*.—The deep, narrow grooves in which the petals lie decrease in depth adorally and die away at the extremities of the petals. The posterior petals are about two-thirds of the length of the anterior pair. The pore-fields extend along the sloping sides of the grooves, the perradial tract coinciding with the floor of the groove. The posterior petals are very slightly curved, the concavity being directed to the antero-posterior axis. The anterior petals have a very slight sigmoid curvature and are much more divergent than the posterior petals. For more than two-thirds of their length they have a slight curve with the concavity directed to the anterior, at their outer extremity they have a very slight curve in the opposite direction. The pores in both anterior and posterior petals are circular, those of a pair separated by a distance equal to their own diameter. The pairs are separated by ridges which probably bore a line of minute granules. The pore-fields and the perradial tract are about equal in breadth at the mid-lengths of the petals. From there, both the pore-fields and the perradial tract contract slightly adorally, while adapically the pore-fields contract but the perradial tract remains of almost uniform breadth.

*Interambulacra*.—The posterior interambulacrum on the superior surface sub-carinate. The other interambulacra on the same surface prominent and rounded between the sunken amb. petals. The mid-zonal plates each bear a small nodosity situated about one-third of the distance between the interradiial and the adradial sutures and near the adapical sutures, and thus there are two series of these little prominences in each interambulacral area. They are largest at the ambitus, becoming less prominent and dying out adapically and adorally. Those of the posterior interradius no doubt outlined the posterior face of the test. On the

oral surface interradius 5 is prominent and rounded and bears a small nodosity near its posterior end. There is evidence of normal heteronomy in interradius 1 on the oral surface.

Peristome.—Transverse diameter 6 mm. The posterior margin is broken away. The anterior margin is semicircular and has a slightly raised rim. Distance of anterior margin from anterior vertical plane about 10 mm.

Periproct.—Only the outline of the left half is preserved. Situated at the top of the posterior face, it is evidently vertically elongate with length about 5.5 mm. and breadth probably about 3 mm.

Ornament.—On the upper surface the tubercles are largest on the sides of the anterior groove. On the oral surface, in the interambulacra near the peristome, they are still larger and have a small mamelon on a crenulated boss standing centrally or eccentrically on a scrobicule, which is raised aborally but which merges into the level of the test adorally. The scrobicules are surrounded by a single ring of miliaries. These tubercles are no doubt those described by POMEL as tubercles *à petit socle oblique*.

A peripetalous is present. It crosses the anterior sulcus about the level of the ambitus (about 21 mm. from the apical disc measured along the groove). It curves gently round the test past the ends of petals II, IV, then turns sharply adapically into interambulacra 1 and 5 for a short distance only, when it makes re-entering angles and runs in straight lines to the ends of petals I and V. It crosses the posterior interradius in an almost straight course between the ends of I and V at a point about 14 mm. from the apical disc.

Affinities.—I have some hesitation in ascribing this species to the genus *Opissaster*, for it appears to have only some of the characters of *Opissaster* and others more suggestive of *Hemiaster*. Typical *Hemiasters* have ethmophract apical systems, but Eocene *Hemiasters* or *Trachyasters* (see P. M. DUNCAN \* and F. A. BATHER †) have ethmolysian apical systems, and it is between *Trachyaster* and *Opissaster* that the present species appears to fall. According to J. LAMBERT,‡ *Opissaster* is merely a sub-genus of *Trachyaster*, but from examination of POMEL's descriptions and figures of *Opissaster polygonalis*, Pomel,§ and *Trachyaster globulus*, Pomel,§ the type species of these genera, this does not appear to be so. In *Opissaster* the ambulacral petals are deep and the anterior pair flexuous as in *Schizaster*, whereas in *Trachyaster*, as in *Hemiaster*, the ambulacral petals are comparatively shallow and the anterior pair almost straight and very divergent.

One would suppose, therefore, that the nature of the ambulacral petals, being a point of importance, would settle the generic position of the present species, but this is not unquestionably so. The ambulacral petals in the present specimen are narrow and deeply excavate as in *Opissaster*; they are, however, only slightly flexuous and are more divergent than is common in that genus. Furthermore, the apical disc is situated anteriorly to the centre (.4 of the length from the anterior vertical plane), and thus the specimen differs from *Hemiaster* in which it is sub-central and farther from *Opissaster* in which it is usually to the posterior of the centre. The apical system has four gonopores, a usual occurrence in Eocene *Hemiasters* (*Trachyaster*). This is not, however, an argument against *Opissaster* in which two is the more usual number.

Most of the tubercles are situated on obliquely raised scrobicules, the tubercles *à petit socle oblique* of POMEL and the presence of such tubercles appears to have been considered

\* DUNCAN, 1889. *Loc. cit.*, p. 229.

† BATHER, 1904. *Loc. cit.*, p. 297.

‡ LAMBERT, 1915. "Desor. Echinides terr. néog. bassin Rhône," fasc. iv, *Mém. Soc. Pal. Suisse*, vol. xli, p. 155.

§ POMEL, 1887. *Loc. cit.*, p. 106, A, pl. ix, figs. 1-5; and p. 109, A, pl. ix, figs. 9-13.



a possible means of distinguishing "*Schizasteriens*" from "*Hemiasteriens*" (*vide* LAMBERT).<sup>\*</sup> This distinction would no doubt hold good in the case of typical *Hemiasters* which have ordinary scrobiculate tubercles, but with Eocene *Hemiasters* (*Trachyaster*) it is not so, for according to POMEL's diagnosis of *Trachyaster*, the tubercles in that genus are oblique. According to LAMBERT,<sup>\*</sup> the tubercles à *petit socle oblique* are not a reliable distinction, as the obliquity of the tubercles is a character capable of gradation. In *Trachyaster* the tubercles with oblique, raised tubercles were probably evolved from the ordinary scrobiculate tubercles of the typical *Hemiasters* along with the evolution from ethmophract to ethmolysian apical systems. According to R. FOURTAU,<sup>†</sup> tubercles which are "*excentrique—sur leur socle*" are characteristic of *Schizaster* and *Opissaster*, and distinguish them from *Hemiaster*. In the present specimen some of the tubercles are situated eccentrically on their obliquely raised scrobicules while others appear to be central, but whether this is a point in favour of *Opissaster* is doubtful.

On the whole it seems best to regard the species as an *Opissaster* with an anteriorly situated apical disc. The species it seems to resemble most is *Opissaster lamberti*, Fourtau,<sup>‡</sup> from the M. Eocene of Egypt, and this species also is evidently not a typical *Opissaster*. The ambulacral petals II and IV are said to be very divergent and slightly arcuate at their extremities, and the species is compared with *Trachyaster heberti*, Cotteau, and not with any other species of *Opissaster*. The figured specimen of *O. lamberti* is crushed, but its ambulacral petals appear to be wider and its pore-fields relatively wider than those of *O. farquharsoni*.

<sup>\*</sup> LAMBERT, 1907. "Descr. des Echinides foss. de Barcelone," pt. 2 Mioc., *Mém. Soc. Géol. France*, Pal. 14, fasc. 2-3, footnote, p. 100.

<sup>†</sup> FOURTAU, 1920. "Catal. Invert. Foss. de l'Egypte," *Geol. Surv. Egypt*, Palæont. Ser. No. 4, Terr. Tert., pt. 2, p. 77.

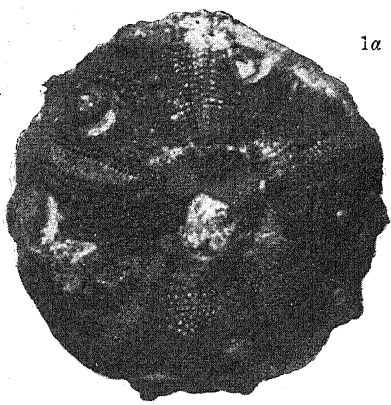
<sup>‡</sup> FOURTAU, 1912. "Notes sur les Echinides Foss. de l'Egypte," iv, *Bull. Institut Egypt*, ser. 5, t. v, p. 173, pl. iv, fig. 4.

#### EXPLANATION OF PLATE.

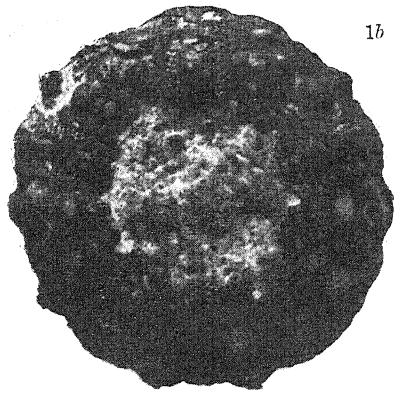
1. *Acrosalenia* (*Metacrosalenia*) *quadrimiliaris*, n. sp.  
FIG. 1A. Holotype. Adapical view. × approx. 2 diam.  
FIG. 1B. " Adoral " " "  
FIG. 1C. " Side " " "
- 2 and 3. *Linthia somaliensis*, n. sp.  
FIG. 2A. Holotype. Adapical view. Approx. nat. size.  
FIG. 2B. " Adoral " " "  
FIG. 2C. " Side " " "  
FIG. 3. Paratype (B.M., E. 18053). A posterior petal. Enlarged.
4. *Opissaster farquharsoni*, n. sp.  
FIG. 4A. Holotype. Adapical view. Approx. nat. size.  
FIG. 4B. " Adoral " " "  
FIG. 4C. " Side " " "
5. *Echinolampas* cf. *amygdala*, Desor.  
FIG. 5A. B.M., E. 18058. Adapical view. Approx. nat. size.  
FIG. 5B. " " Side " " "
- FIG. 6. *Linthia* sp. aff. *insignis*, Mérian.  
B.M., E. 18055. Side view. Approx. nat. size.



ETHEL D. CURRIE on "Jurassic and Eocene Echinoidea from Somaliland."



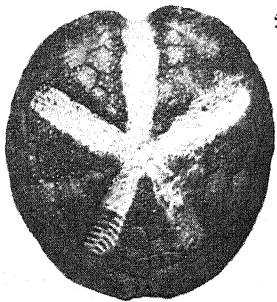
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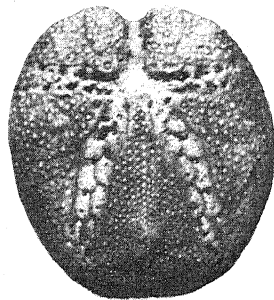
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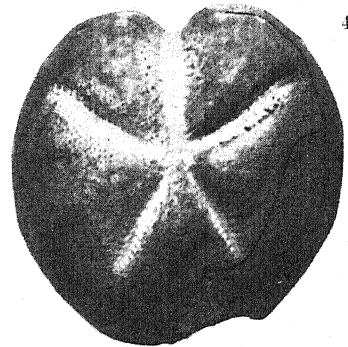
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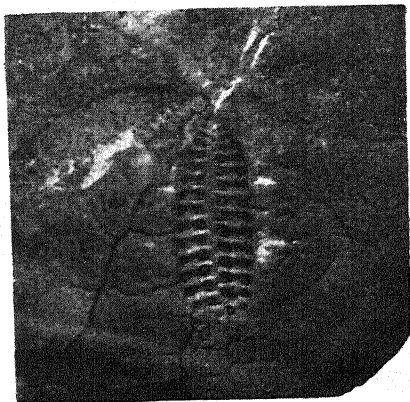
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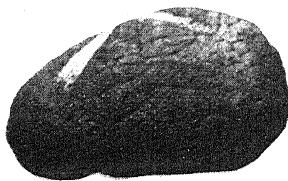
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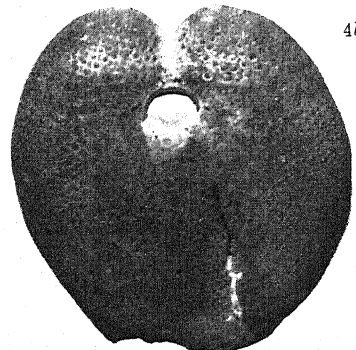
4a



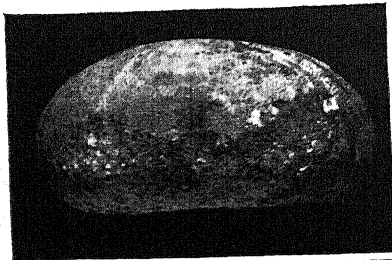
3



2c



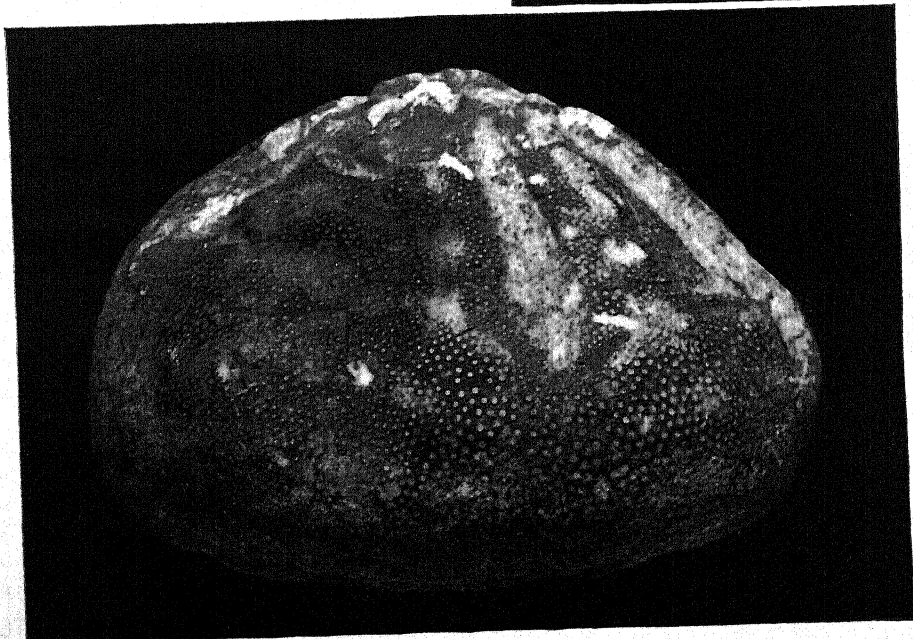
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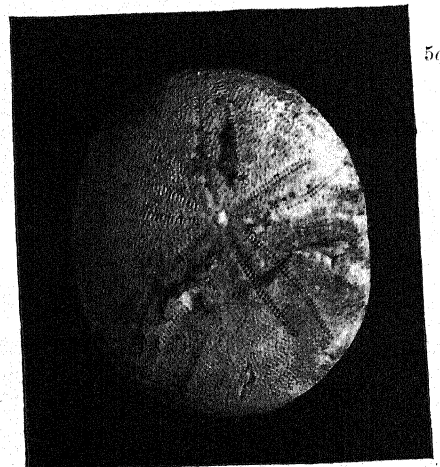
5b



4c



6



5a





- XIX.—Contributions to the Study of the Old Red Sandstone Flora of Scotland. VI. On *Zosterophyllum myretonianum*, Penh., and Some Other Plant-remains from the Carmyllie Beds of the Lower Old Red Sandstone. VII. On a Specimen of *Pseudosporochnus* from the Stromness Beds. By W. H. Lang, D.Sc., F.R.S., Barker Professor of Botany in the University of Manchester. (With Two Plates.)

(MS. received June 6, 1927. Read June 6, 1927. Issued separately October 13, 1927.)

# VI. ON *ZOSTEROPHYLLUM MYRETONIANUM*, PENH., AND SOME OTHER PLANT-REMAINS FROM THE CARMYLLIE BEDS OF THE LOWER OLD RED SANDSTONE.

Among the commonest and most abundant plant-remains in the Carmyllie and Cairnconon Beds of the Caledonian Lower Old Red Sandstone are branched linear axes about 2 mm. in width. These often occur in a fragmentary condition, but more connected portions demonstrating the morphology of the plant are also found. Though often associated with *Parka* and *Nematophyton*, the plant known as *Zosterophyllum myretonianum* is usually readily recognisable by its definite outline and uniform diameter, by its modes of branching, and by the remains of structure which it sometimes retains. As will be seen below, the axis of this plant was traversed by a single median strand that was composed of tracheides. *Zosterophyllum* is thus of special interest as the most ancient vascular plant known from British rocks. Some other plant-remains that may be confused with it have also been met with, though less commonly. These will be briefly considered, not merely for this reason, but on account of the very different and peculiar type of structure they exhibit.

## *Zosterophyllum myretonianum*, Penhallow.

1831. "Narrow leaves of gramineous (looking) vegetables," FLEMING, J., *Cheek's Edinburgh Journal*, vol. iii, p. 86.
1841. "Impressions of more slender form that resemble the narrow parallel-edged leaves of the sea-grass weed," MILLER, HUGH, *The Old Red Sandstone*, p. 179 (2nd ed.).
1857. "Ribbon-like fronds or branches . . . rose by dozens from a common root, like the fronds of *Zostera* . . . resembled a scourge of cords fastened to a handle," MILLER, HUGH, *Testimony of the Rocks*, p. 442.
- "Spike with kidney-shaped leaflets," *ibid.*, p. 445, fig. 122.
- "Parallel stalks, anastomose with each other by means of cross branches," *ibid.*, p. 464, fig. 123.
1877. *Psilophyton* sp., PEACH, C. W., "Notes on the Fossil Plants found in the Old Red Sandstone of Shetland, Orkney, Caithness, Sutherland, and Forfarshire," *Trans. Geol. Soc. Edin.*, vol. iii, p. 151.
1886. ? included in *Psilophyton dechenianus*, Goeppert sp., KIDSTON, R., *Catalogue of Palaeozoic Plants*, pp. 232-235.
1891. "Leaves of *Parka*, b *minor*," DAWSON, J. W., and PENHALLOW, D. P., "*Parka decipiens*, Notes on specimens from the Collection of James Reid, Esq., of Allan House, Blairgowrie, Scotland," *Trans. Roy. Soc. Canada*, vol. ix, section 4, p. 3.
1892. *Zosterophyllum myretonianum*, PENHALLOW, D. P., "Additional Notes on Devonian Plants from Scotland," *Canad. Rec. Science*, vol. v, pp. 1-13, pl. i, fig. 1; pl. ii, figs. 1, 2.
1898. *Zosterophyllum myretonianum*, Penh., REID, J., and MACNAIR, P., "On the Genera *Psilophyton*, *Lycopodites*, *Zosterophyllum* and *Parka decipiens* of the Old Red Sandstone of Scotland," *Trans. Geol. Soc. Edin.*, pp. 368-380, pl. xxi, figs. 1-5.
1902. *Zosterophyllum myretonianum*, Penh., KIDSTON, R., "Note on the Fossil Plants of the Old Red Sandstone of Scotland": The Geology of Lower Strathspey (explanation of Sheet 85), *Mem. Geol. Survey Scotland*, p. 83.
1921. *Zosterophyllum myretonianum*, Penh., ARBER, E. A. N., *Devonian Floras*, p. 12, fig. 22.

The recognition of this type of plant by successive investigators is indicated by the above synonymy. The early references to it by FLEMING and HUGH MILLER emphasise the narrow linear incrustations, with definite parallel edges, which suggested the comparison with *Zostera* that was later embodied in the generic name. HUGH MILLER, who regarded the plant as an Alga, speaks of these linear branches as rising by dozens from a common root, and this will be seen later to be generally confirmed in the sense that the plant had a tufted growth. MILLER nowhere figures the plant as thus described, but in the *Testimony of the Rocks* he included figures of two peculiar specimens, given to him by FLEMING, both of which can now be identified as parts of *Zosterophyllum*. One shows a peculiar anastomosis of linear axes, and finds its explanation in a type of branching frequently met with. Similarly the axis bearing kidney-shaped leaflets will be found to agree closely with the upper parts of the *Zosterophyllum* plant. The specimens represented in MILLER's figs. 122 and 123 are thus properly included in the synonymy.

While MILLER recognised this plant as distinct among the few types in the Arbroath flagstones and as one that did not occur in Caithness, he did not give names to any of the plants. The first identifications of the remains we now call *Zosterophyllum myretonianum* have only to be noted in passing as erroneous. It appears to be the plant on which the records of *Psilophyton* sp. or *Psilophyton princeps* in the Arbroath flagstones were based. It is now clear that there is no evidence of the occurrence of *Psilophyton princeps* at this horizon and that it is only known in Scotland from the Strathmore Beds. Since the plant is not otherwise referred to, it has been assumed to be included among the rather heterogeneous collection of Middle and Lower Old Red Sandstone plant-remains placed under the name *Psilophyton dechenianus* in the British Museum Catalogue of Palæozoic Plants.

About 1890 a collection of Scottish Old Red Sandstone plants was sent to Canada by Mr REID of Blairgowrie. In the paper by DAWSON and PENHALLOW, published in 1891, the narrow linear axes were regarded as the vegetative organs of one of the forms of *Parka decipiens*, which these investigators thought could be recognised. But in the following year PENHALLOW, though he still held that other remains were vegetative organs of *Parka*, distinguished the plant with which we are concerned as *Zosterophyllum myretonianum*.

PENHALLOW not only named the plant and gave a diagnosis of it, but provided the first figures of the branched axes. His description and figures were repeated with some additional remarks by REID and MACNAIR in 1898. These two papers are the most definite accounts of *Zosterophyllum* that have hitherto appeared and are substantially accurate, although, as will be seen, they require amplification and correction in a number of points. It may be noted that both papers, though evidently based on specimens from the Carmyllie Beds, assume that *Zosterophyllum myretonianum* also occurs in the Middle Old Red Sandstone of Caithness. I know of no specimens that justify this assumption.\*

PENHALLOW's description † is as follows:—

“ Genus *Zosterophyllum*, n. gen.

“ Aquatic plants with creeping stems, from which arise narrow dichotomous branches and narrow linear leaves of the aspect of *Zostera*. Fruit, an ovoid or spherical sporangium (?), produced on short pedicels, without subtending bracts, from a single axis, the whole forming a loose spike.

“ Lower Devonian of Myreton, Scotland, REID.

\* SALTER's “ Rootlets with Lateral Tubercles,” cited by PENHALLOW, are now known as *Hostimella racemosa*.

† *Loc. cit.*, p. 12.



"*Z. myretonianum*, n. sp.—Stem and branches, 2 mm. in diameter. Leaves, linear 1.5–2 mm. wide, often showing an inconspicuous veining. Sporangia, 2.5–4 mm. broad, round, or ovoid. Superficial structure, none."

In PENHALLOW's account certain axes bearing ovoid or spherical bodies are rightly assigned to *Zosterophyllum* on grounds of their close association, and the question is raised as to whether they are the sporangia. In REID and MACNAIR's paper this interpretation is assumed without question, and the peculiar form of branching giving the appearance of an anastomosis is also referred to the plant. While this latter feature is not shown in the specimen figured by PENHALLOW, his illustration is an excellent representation of the other types of branching met with in the plant and of the general arrangement of the axes. This figure is repeated by REID and MACNAIR and by ARBER, and is thus readily accessible. On the other hand, PENHALLOW's distinction of "leaves" and "stems" arising from a rhizome, and his interpretation, as parallel venation, of the linear marks often shown by the remains of incrustations adhering to the rock, will be found to be erroneous. The isolated discoid bodies \* are not to be included with *Zosterophyllum*.

There has been no later investigation of *Zosterophyllum* so far as I am aware. But in 1922 ARBER, when giving a diagnosis and repeating some of PENHALLOW's figures, indicated by queries how many points he regarded as doubtful, and concluded by remarking that "this fossil is at present wholly obscure."

Having surveyed the history of investigation of *Zosterophyllum myretonianum*, an account will be given of what has been ascertained by the study of specimens collected at various localities in Forfarshire. The most useful and abundant material was obtained from Balgavies Quarry near Auldbar Road station, from Clocksbriggs Quarry, and from Balmashanner Quarry, just south of Forfar. Specimens collected by Dr KIDSTON from Balruddery Den and other exposures near Dundee, and now placed in the Kidston Collection, have also been examined. The results have been supplemented by an inspection of specimens in the Powrie Collection in the Royal Scottish Museum, Edinburgh, and in the Mitchell Collection, now preserved in the British Museum (Natural History). While confirming the observations made on the material available for detailed study, these collections have not revealed any important additional facts. The characters of the various types of remains belonging to this plant are very uniform from whatever locality in the Carmyllie or Cairnconon Beds they have been obtained.

Since the remains of *Zosterophyllum* are usually fragmentary, though often associated together in quantity, it will be well to start with a specimen that demonstrates the connection of various types of the fragmentary remains as parts of one plant and gives some idea of its mode of growth. The instructive specimen represented  $\frac{2}{3}$  natural size in fig. 1, came from a large block of rock found in Balgavies Quarry. The surface figured shows a tuft of the plant with elongated axes radiating out from a confused basal region. These straight axes were 15 cm. or more in length and were sparingly branched, either dichotomously or laterally (cf. figs. 4, 5). The lateral branches often stood out a short distance, almost at right angles, before bending upwards to lie almost parallel with the relatively main axis. None of the few branchings at first seen in this specimen exhibited the peculiar type, with a backwardly directed limb, that is frequently met with in fragmentary specimens (cf. fig. 7). It seemed desirable, if possible, to demonstrate this characteristic type of branching in this particular pure and relatively complete specimen of *Zosterophyllum*. On laying bare a further portion of the tuft by splitting off a piece of the rock, a clear example was exposed, and is seen on the

\* *Loc. cit.*, p. 11, pl. ii, fig. 3.

right-hand side of fig. 1 at *x*. The counterpart of this region is represented of natural size in fig. 2 and shows the branching more clearly, though of course reversed. From near the base of the ascending branch there is another branch, directed obliquely backwards, and this appears almost at once to give off another ascending branch, only the base of which is visible. While better examples have been found isolated (*cf.* figs. 7-9), the one in fig. 1 suffices to relate this type of branching to the complete plant. Since it lay at about the level of the basal region of the tuft, it seemed a reasonable supposition that it characterised the lower or rhizomatous portion of the plant; this is supported by the relation of the system of branches in other specimens (*cf.* fig. 8) and by the prevalence of other types of branching in the elongated erect axes. But, as shown by fig. 6, a backwardly directed branch may occur in them also. In their distal portions practically all the elongated axes show a further morphological differentiation, in that they bear stalked reniform appendages radially arranged. These are seen in relation to most of the axes in the upper part of fig. 1, and a portion of this region is represented of natural size in fig. 3. As exposed on splitting the stone, the appendages exhibit various shapes and may even appear as rounded bodies lying alongside the axis. Whatever their nature is, and so far proof that they are sporangia has not been obtained, there is no question of their belonging to the *Zosterophyllum* plant, and their demonstration in this specimen justifies the identification of such axes with appendages when met with as isolated fragments.

The value of the relatively complete specimen represented in fig. 1 is that it provides evidence that various structures, often found in separate fragments, really belong, as might be assumed, to the one plant. These parts of the plant of *Zosterophyllum*, which as will be evident from the historical survey have long been known as isolated structures, may now be considered in further detail.

The stems or axes vary in width round about a mean of 2 mm., some being 3 mm. wide, while others are only slightly over 1 mm. They often show no indication of structure, existing only as flattened black films, which are naturally more or less split when exposed on the surface of the stone. When, as is not infrequently the case, the compressed axis had its surface thrown into wrinkles or folds, the organic material may remain adherent along irregular lines. This gives the appearance of a longitudinal striation that was erroneously interpreted by some investigators as indicating parallel venation. More satisfactorily preserved axes, especially when on a surface of fine-grained rock, may show a distinct median strand. While this was detected in some of the dark incrustations of the specimen represented in fig. 1, it is very clearly seen in the branched axes shown in figs. 8 and 9. These afford excellent examples of the peculiar type of branching in which while one division of the branch turns upwards another turns downwards; the latter may, like a rhizome, give off other ascending branches. In this specimen, as is best seen in the enlarged photograph (fig. 9), a dark median strand can be followed in the relatively main axis and subdividing in relation to the branching.

Other examples of the type of branching shown by this specimen are afforded, as has already been pointed out, by figs. 2, 6, and 7, while lateral branching without a backward branch is seen in fig. 4 and dichotomous division in fig. 5. With a little experience these appearances of the axes are quite characteristic and enable even fragmentary remains to be identified in most cases.

In all the material so far met with the axes of the plant, which were doubtless cylindrical, are compressed into flattened films that represent the remains of the organic material. Sometimes this has broken down into small angular fragments, but when it has remained continuous, portions can be dissolved out from the matrix by hydrofluoric acid as a coherent film, that

can then be macerated in nitric acid and potassium chlorate. The organic material may also be transferred from the rock to a film of cellulose either directly or after preliminary maceration on the stone. While many of the preparations thus made show no indications of true structure and merely present an irregular surface due to the indentation of the grains of the matrix, a few of them have yielded information as to the histology even of this unpromising material.

Thus the median strand already mentioned as seen with the naked eye in specimens on the rock is evident as a dark band in the macerated film, a portion of which is shown in fig. 10; this came from the same block as fig. 1. A similar dark band is visible, without maceration, in the fragment of axis above and to the right in the transfer represented in fig. 15. From these and other specimens it was found that the median strand in its flattened condition was about  $\frac{1}{4}$  mm. wide. It might safely have been assumed that this median strand was the vascular system of the cylindrical axis of the plant, though in most cases it has lost all trace of structure and lies like a dark stain against the equally structureless yellow film which is derived from the cuticle. From some fortunate preparations it has, however, been possible to obtain evidence to prove that the strand was composed of tracheides.

This was the case along portions of the edge of the strand in the specimen represented in fig. 10, although most of the strand had lost all trace of structure. In fig. 11, which shows a small portion of the edge of the strand highly magnified, a few isolated elements are seen that have their walls thickened with annular bands. This specimen had been macerated, but in a transfer of the fragments on the surface of a piece of rock similarly thickened tracheides were found composing a vascular strand within one of the axes. This strand in the un-macerated condition was too opaque to be figured, but an adjacent fragment on the transfer, represented in fig. 12, shows portions of a number of the thickened elements. In the examples that could be measured these ranged from 15 to 22 $\mu$  in width. Their ends were not clearly seen. The thickening appears to consist of fairly closely-placed rings and has not been seen to be connected as a continuous spiral.

The cortical tissues have not been preserved in any of the specimens that have been examined. They are usually replaced by amorphous brown material that clears or disappears on maceration. Some preparations suggest a hypodermal layer of elongated thick-walled cells, but the presence or distribution of this has not been definitely established. As already mentioned, the yellow film, that may be all that remains of the axis after maceration and probably represents the cuticle, usually conveys no information as to the cellular structure (fig. 10). In a few cases, however, the walls of the epidermal cells have been preserved and give the outlines of the cells clearly. A portion of such a specimen is represented in fig. 13 and shows how the cell-walls, though clearly traceable, are broken into fragments and could only have been obtained for examination by the transfer method. The cells differ from one another somewhat in size and shape. In this preparation, which there is some reason to think came from the lower rhizomatous region of the plant, they are about 100 $\mu$  long and half as broad.

Stomata were absent from this portion of epidermis and no clear examples, showing the guard cells, have been seen either in the few pieces of epidermis found or in the less altered pieces of cuticle. The amount of favourable material thus examined is, however, so small that no weight can be attached to this negative result. Indeed an indication of the presence of stomata is afforded by a well-preserved film of cuticle that had traces of the epidermis beneath. This specimen showed fairly regularly spaced, brown, linear markings on the cuticle that were strongly suggestive of ill-preserved stomata as found in fossil cuticles (fig. 22).



It may be mentioned that the cuticle as shown by the preparation just referred to was strongly developed. As seen in optical section it measures  $2\mu$  in thickness.

The general appearance and the position in the plant as a whole of the axes with appendages was noted in connection with the specimen shown in fig. 1. Practically every one of the erect elongated axes in this bore appendages in its distal portion. The study of material from this block and of a number of isolated specimens found elsewhere has shown a general agreement in the morphology of this region of the *Zosterophyllum* plant. It will be sufficient to refer to the specimens illustrated in figs. 14–20 without unduly multiplying examples.

Figs. 14, 15 show the information that can be obtained by the transfer method. In fig. 14 an axis with appendages is represented as seen on the stone, enlarged three and a half times. The course of the axis can be traced and the diversity of shape assumed by the appendages recognised. The details of the same specimen are seen more clearly when it is transferred and viewed clear of the matrix as in fig. 15, which is enlarged four times, and is, of course, reversed as compared with the specimen on the rock. Some nine appendages are borne on this short length of axis, which is broken off above. The two lowest exhibit a conical tubular form that is not infrequent and will be considered further below. The next is seen from behind in fig. 15 as it lies against the axis and shows its true shape, a stalk-like region widening into a kidney-shaped expansion. The next, on the left in fig. 15, shows the same regions, though the expanded portion is exceptionally small. The succeeding appendage, on the right in fig. 15, resembles the lowest two, being seen from the side: on the stone it appeared as a curved structure with an oval widening to the adaxial side, while the transfer showed that the expanded portion was folded round and included some of the matrix. The next appendage is obscured in the dark mass in fig. 15, but in fig. 14 is seen as a stalked reniform body lying over the axis. Then follow two imperfect appendages, one to either side, while the last one above the broken-off axis shows the stalk widening into the blade-like expansion. If the position and succession of the appendages in this specimen are considered, their radial arrangement will be evident.

A number of other similar axes, derived like that just considered from the same block as the plant in fig. 1, have been transferred. One of them, represented enlarged four times in fig. 16, is of special interest since it shows a vascular strand in the main axis and the departure of a trace to one of the appendages, that on the right about half-way up the figure. Another trace is seen above and to the left that supplied an appendage higher up that was seen on the rock, but not included in the transfer.

The specimen from Clocksbriggs Quarry represented of natural size in fig. 17 bore some eight appendages more widely spaced than in the preceding examples. Only the topmost of these, above the end of the incomplete axis, shows the widened region from the face view. The others are seen from the side in various ways. One, on the right-hand side about one-third way up, shows the conical form, in this case represented by a hollow in the stone. The appendage almost opposite to this and some of the others have the appearance of curved structures bearing an oval body adaxially to its distal region. Practically all the appendages in this specimen are seen in profile, and the resulting appearances are discussed below.

On the other hand, most of the appendages of the specimen represented of natural size in fig. 18 and enlarged three times in fig. 19 are seen from either the front or the back. It was found at Peterden near Dundee by Mr M'NICOL and given by him to Dr KIRSTON. The flattened ribbed axis is about 9.5 cm. long and bears some twelve appendages. The lowest are rather small and appear conical; they may have been more rudimentary than those in the upper two-thirds. These showed very clearly the short, wide stalk bulging outwards

somewhat as it passes into the reniform expanded part that is bounded by a rather distinct rim (fig. 19).

The outline of the appendages when seen from the adaxial or abaxial sides explains the form of detached specimens that are to be found among the fragmentary remains of *Zosterophyllum*. One such is represented in fig. 20 and appears kidney-shaped, the basal concavity representing the place of attachment of the stalk. The convex margin is, as usual, distinct, appearing like a thickened rim. This specimen had been macerated on the stone and transferred to a cellulose film, cleared and mounted in balsam, and could thus be microscopically examined. While a certain difference was evident between the rim and the central region, neither in this nor in a number of similar preparations could evidence be obtained that the difference was due to spores enclosed by the wall of a sporangium.

The indications afforded by the specimens described and by others that have been examined all seem to point to the appendages, even before preservation, having been somewhat flattened structures with a stalk-like region widening out into the kidney-shaped region. This true form is presented whenever the appendage is seen from the front or behind, whether as an isolated structure or as borne on the faces of an axis turned upwards or downwards as it lay on the rock. The other and very dissimilar appearances presented by appendages standing out from the sides of an axis and seen in profile, though at first sight significant, can all be understood as due to such flat appendages having been compressed so that the two halves are folded together. If such a specimen is split through in the median plane, it may give the appearance of a curved linear structure with an oval body placed adaxially to its distal portion. The infolded appendage may also appear like a conical tubular body enclosing matrix, or, if the latter is removed, as a conical depression in the stone. This diversity of appearance is not only comprehensible, but affords corroborative evidence that we are dealing with what were originally relatively flat organs, and not with stalked globular bodies that have been flattened in fossilisation.

The reniform expansion measured about 3.5–4.0 mm. across in a number of the best examples seen.

The conclusion as to the original shape of the appendages to which the various facts seem to lead is in line with the description given by HUGH MILLER of the specimen discovered by FLEMING. The reniform appendages were by him interpreted as leaflets, and the suggestion was made that the plant might be a fern. On the other hand, PENHALLOW regarded the examples he examined as stalked spherical bodies that had been flattened; he suggested that they were the sporangia and that the whole structure was the fruiting spike of the plant.

This is the view to which I have found palaeobotanists, on being shown the specimens figured here, are at once led. Indeed, when the whole organisation of *Zosterophyllum* is considered the most natural interpretation of the appendages would seem to be that they are stalked sporangia, which, even in the living state, were rather flat structures presenting a reniform outline when viewed tangentially. I have, however, failed to obtain critical evidence to show that the reniform expansions were sporangia. None of the examples removed from the rock by transfer methods, whether after preliminary maceration or without this, have shown any trace of spores. It is true that none have shown structure as well preserved as is occasionally met with in the superficial tissues of the axis, but from the experience afforded by other plants it might have been expected that spores would have been recognisable either within the sporangia or in their immediate neighbourhood.

Whatever better preserved specimens may reveal, the only justifiable conclusion on our present knowledge is that the reproductive organs of *Zosterophyllum* are not known with

certainty. It would be an assumption to identify the reniform appendages as sporangia, though this may ultimately prove to be their nature.

Under the circumstances, it seems worth while, without attaching much importance to it, to place on record a specimen of peculiar appearance from Balruddery Den that is in the Kidston Collection. What appeared to be a lateral appendage lay beside an axis with the general characters of *Zosterophyllum* (fig. 21). The lateral structure, which is enlarged three times in the figure, showed on the side of the impression towards the observer, marks suggesting some six linear bodies, standing erect from the curved base. Slightly further in the stone what looked like the tips of a parallel series were visible. The appearance is accurately represented in the photograph. There is, of course, nothing to show that the linear bodies were sporangia, though their appearance and arrangement suggest this.

The chief points now known regarding *Zosterophyllum myretonianum* may be briefly summarised.

Though the remains are usually fragmentary they are abundant and generally distributed, and the more complete specimens justify a conception of the plant as of gregarious and tufted growth and attaining a height of at least 15 cm. It consisted of a system of branched axes, and there is reason to distinguish a lower rhizome-like region from which erect axes grew. The peculiar type of branching with backwardly or horizontally growing ramifications from the base of a lateral branch seems to be specially related to the rhizomatous region though not confined to this. The erect axes, which as a rule show sparing lateral or dichotomous branching, are, like the rhizome, without appendages in their lower regions, but higher up they bear characteristic, radially arranged, stalked, reniform appendages. While the position of these strongly suggests that they may be the sporangia, no proof of the presence of spores has been obtained, and the nature of the reproductive organs is not at present known with certainty. The axes of the plant are about 2 mm. wide and had a thick cuticle over the epidermis. Stomata have not been clearly demonstrated, though there are indications that they were present. Nothing is known as to the structure of the cortex, but the presence of a central vascular strand about  $\frac{1}{4}$  mm. wide has been demonstrated and is found to consist of tracheides with close annular thickening. This vascular strand follows the course of the branching of the axes and also gives off a more slender trace to each of the appendages.

The plant is of special interest as the earliest known vascular plant from British rocks. Its remains occur along with those of *Nematophyton* and *Pachytheca*, and both *Cephalaspis* and *Kampecaris* have been seen on the same slabs of rock with its remains.

The facts summarised above have all been ascertained by the study of the remains that occur in the Carmyllie and Cairnconon Beds of the Caledonian Lower Old Red Sandstone. Little can be said as to the occurrence of plant-remains that agree in detailed features with this fairly fully-known type from other localities and horizons.

I have seen a single specimen with the characteristic branching from the Lower Old Red Sandstone of England. It was collected on Caldy Island and is in the collection of the Geological Survey (No. Pr. 2813). This is probably satisfactory evidence of the occurrence of the same plant. Reniform structures that are very similar to those of *Zosterophyllum* have been found in the Lower Old Red Sandstone of Breconshire and are there regarded by Dr HEARD \* as the sporangia of the plant he distinguishes as *Goslingia Breconensis*.

A most striking and close agreement with the peculiar type of branching that is found in *Zosterophyllum* is exhibited by some specimens from the Upper Devonian of Perry, Maine,

\* "On Lower Old Red Sandstone Plants showing Structure from Brecon (South Wales)," *Proc. Geol. Soc.*, Dec. 1, 1926. I am indebted to Dr HEARD for information as to his results.



that are figured and described by SMITH and WHITE \* under the name ? *Psilophyton alcicorne*. We may hesitate to regard this as proof of specific identity, but it is clear evidence of the existence of a plant of similar morphological construction.

Close comparisons of the morphology of *Zosterophyllum* with that of other plants, on which alone conclusions as to its affinity can be drawn, are impossible until the doubtful points as regards the reproductive organs of the plant are cleared up. But the indications are that *Zosterophyllum* will find its place among the relatively simple Psilophytales of the general type of the Rhyniaceæ. Comparison may especially be made with *Hicklingia Edwardi* † from the Middle Old Red Sandstone of Scotland. The two plants agree in the tufted growth, and in the presence of what are presumably or possibly sporangia borne laterally on short stalks upon the upper regions of the erect axes. But there are sufficient differences as regards both the branching and the size and shape of the structures that are presumably sporangia to keep the two plants generically distinct.

*Some other Linear Remains from the Carmyllie Beds.*

The parts described above have been shown to occur in connection in the plant of *Zosterophyllum myretonianum*. While there are, of course, numerous linear fragments that do not afford characters which are decisive for their reference to this plant, they are probably derived from it, and no evidence has been obtained to justify the recognition of more than the one specific type. This vascular plant is very widely distributed and abundant throughout the Forfarshire-Kincardineshire area.

It was pointed out in a previous paper ‡ that narrow, branched specimens of *Nematophyton* are sometimes met with, but these can be distinguished by their very different construction of parallel tubes.

A preliminary description has now to be given of some incrustations of narrow, branched axes that cannot be referred to either *Zosterophyllum* or *Nematophyton*, though their peculiar structural features have more in common with the latter type. Our knowledge of them depends as yet on a few specimens and it is not certain that we are dealing with a homogeneous group of remains though this seems probable. A brief account of the main specimens will serve to distinguish them from the finer branches of *Zosterophyllum*, with which they might be confused, and will prepare the way for obtaining further knowledge of them.

Among the specimens kept by Dr KIDSTON for future study were two pieces of rock from Balgavies Quarry, the surface of which bore numerous linear dark incrustations. The appearance of a portion of one of these specimens is represented of natural size in fig. 23. The dark incrustations were about 1 mm. in breadth and some of the pieces were over 2 cm. long. Most of them were unbranched, but one or two showed indications of branching. The blackish-brown films were readily detached from the surface of the stone. The natural assumption was that they were fragments of linear axes and possibly of *Zosterophyllum*, but on portions being macerated the surprising fact became evident that the linear films were entirely composed of small spores, and that we were dealing with compressed spore-masses of exceptional size. A portion of a macerated specimen is magnified twenty times in fig. 24, and this shows the texture dependent on the spores, though the magnification is too low to show them individually. A portion of the margin of a similar macerated spore-mass is,

\* U.S. Geol. Survey, Professional Paper No. 35, p. 64, pl. v, figs. 1, 2.

† KIDSTON and LANG, *Trans. Roy. Soc. Edin.*, vol. liii, p. 405, pl.

‡ *Trans. Roy. Soc. Edin.*, vol. liv, p. 795, pl. ii, fig. 16.

however, magnified two hundred times in fig. 25. This shows the individual spores which measure about  $35\mu$ . No evidence of their association in tetrads has been obtained.

Further light was thrown on these spore-masses by some specimens of narrow linear, branched axes collected at Balgavies Quarry. In width and mode of branching they appeared different from *Zosterophyllum*, and when transfers were made it was ascertained that the type of construction was fundamentally different. The general appearance of these fragmentary axes, as transferred to a surface of canada balsam, is seen in fig. 26 enlarged three times. The structure was only visible at favourably preserved spots, but was there found to consist of branched filaments (fig. 27) and not of a true cellular tissue. What was still more instructive was that linear masses of spores, similar to those described above, could be seen to be enclosed within an investment of this peculiar filamentous construction. The presence of the layer of balsam in this preparation was found to render photographic illustration of these details, which were clear on microscopic observation, impossible. The fragments that showed these features were 1-1.5 mm. broad and presented indications of a rather divergent dichotomous branching.

Similar fragments were found more abundantly at Clocksbriggs Quarry and showed the same structure on being transferred. A portion of a transfer from this locality, including the region of branching of an axis, is enlarged twenty times in fig. 28. A more complete specimen showing the branch-system on the rock enlarged three times is represented in fig. 29. The narrow axis is rather laxly divided several times in a dichotomous manner that approaches a sympodium. A separate fragment, to the right above, shows an appearance that has been several times observed, of ending in a wider oval expansion.

The most connected and perfect hand-specimen that is naturally to be placed with this group of remains, though its histological structure has not been ascertained, was also found in the same quarry-tip at Clocksbriggs. It is represented of natural size in fig. 30 and enlarged five and a half times in fig. 31. There is a short length of axis about  $\frac{3}{4}$  mm. wide, and this appears to bifurcate at its upper end, one branch being broken off short. The other repeatedly dichotomises to give a small tuft of branches that are under  $\frac{1}{2}$  mm. in width. The ends of some of the ramifications, including some that are sympodially displaced so as to appear lateral, appear enlarged. The nature of this enlargement is, however, obscure, partly because it is associated with a curvature of the end of the branch. It did not appear desirable to risk destroying this unique little specimen on the chance of obtaining evidence as to its structure. But the general appearance, size, and mode of division of its branches is such that it is reasonable to regard it as of the same nature as the fragments from the same rock that have shown the filamentous type of construction.

Summarising the above facts, it seems to be clear that another type has to be added to the limited flora of the Carmyllie Beds. The remains so far known are dichotomous branch-systems of slender axes. The characteristic structure of the peripheral region of the axis consists of much-branched tubes or filaments. Nothing is clearly ascertained as to the vegetative structure of the central region, but this may be occupied by a coherent mass of small spores.

Until further specimens are obtained and investigated, it is advisable, while clearly distinguishing this type, to leave it without name and as *incertae sedis*. Its recognition is an indication that there are possibilities of adding to the flora of this horizon of the Lower Old Red Sandstone. The structural evidence is against any association of it with *Zosterophyllum*. The structure differs in details from that known in the larger axes of *Nematophyton*, though it has much more in common with this. It is to be borne in mind that the ultimate ramifications of *Nematophyton* are not known, nor do we know anything of the reproductive organs of the plant.

## VII. ON A SPECIMEN OF PSEUDOSPOROCHNUS FROM THE STROMNESS BEDS.

The remarkable specimen of which an account is given here is now preserved in the Stromness Museum. Though it was only presented to the Museum last year, it was found a number of years ago by Mr ROBERTSON, when a quarry near his farm of Lyking was being worked. My attention was directed by Mr DAVID LAING to a note in the *Orcadian* of 28th January 1926 regarding it, and I examined it when at Stromness during the summer. I am indebted to Mr MARWICK for permission to remove the specimen to the adjoining photographic studio, and to Mr HOURSTON for taking the photograph reproduced in fig. 32. This represents the specimen about one-third natural size, as it is exposed on the surface of a thick slab of flagstone. The horizon of the quarry in which it was found is that of the Stromness Beds or Achanarras zone of the Middle Old Red Sandstone.

As the figure shows, the specimen consists of a main axis tapering gradually from a wider rounded lower end and dividing into four equal and diverging branches. Its total length is 34.5 cm., the unbranched portion from the base to the region of branching being about 25 or 26 cm. The maximum width near the base is 4 cm., and on passing up the axis narrows to a width of 2.5 cm. just below the region of branching. Above this, across the connected bases of the branches, the width becomes greater, about 3 cm. The branches are all similar and are about 1 cm. wide. The free portions of the branches, none of which in the length preserved shows subdivision, are about 5 cm. long.

The specimen has a rounded lower end which cannot, however, be assumed to be the true surface boundary at this region, though this is possible. There are no indications of any rooting or attaching organs. Nor are there any appendages throughout the length of the main axis or its branches which might be interpreted as leaves. We have to deal with a cast or incrustation of a very peculiarly branched axis, the specimen being evidently incomplete above and almost certainly so below.

There are remains of a continuous layer of carbonaceous material that has been almost completely worn off from most of the surface and partially so throughout. Where best preserved, as in the region of divergence of the branches, only an indistinct ribbing is visible. On the other hand, a parallel ribbing is evident on the branches, the ridges being about 1 mm. apart. The ribbing is indeed traceable over the whole specimen and becomes particularly clearly marked near the base. At places the ribs give the impression as if they were due to more deeply entering lines from a continuous outer coal layer.

The above description with the accompanying figure gives the features of this specimen which could be ascertained from an examination of it with the aid of a lens in the Museum. It is doubtful whether much additional information could have been obtained by more detailed examination.

The characters noted—the gradual diminution in thickness from the base upwards of a main axis, the division, practically at the same level into a few diverging main branches, the absence of any definite appendages, and the ribbing of the surface—taken together have not been met with in any specimen hitherto described from the Old Red Sandstone of Scotland. The special interest of the specimen lies in its unmistakably close agreement with a type of plant of which numerous and more complete examples have been described from the Middle Devonian of Bohemia and which is known as *Pseudosporochnus Krejčí*.

Originally distinguished by Krejčí, this fossil was described by STUR as an alga, but the fullest description, based on abundant specimens, a number of which are figured, is that given



by POTONIÉ and BERNARD.\* While many of their specimens agree in size with that under consideration here, they produce evidence showing that examples of much greater size are met with. Points of detailed agreement are the enlarged basal region and the divergence of a small number of branches in an almost palmate fashion from the summit of the gradually narrowing main axis. To this may be added the indication of longitudinal ribbing, which, however, POTONIÉ regarded as "knorrioid" in nature, though he also compared it with the striation in a Calamite.

Some of the specimens figured by POTONIÉ and BERNARD bore narrow appendages from or near the basal region, and these investigators compared them with "roots." There is no trace of them in the Scottish specimen and they are completely wanting in some of those from Bohemia. Nothing is known in detail regarding them.

POTONIÉ and BERNARD further demonstrated, from fortunate, more complete specimens, that the few main branches became more and more subdivided. They regarded the branching as essentially dichotomous throughout, but with a sympodial development causing the finer branch-systems to appear laterally placed. They showed that the palmate division at the summit of the main axis is based on dichotomous branching. The repeated subdivision differs from the relation of leaves to a stem, and there appears to be no approach to this grade of organisation in the plant. Certain of the ultimate subdivisions widened slightly at their tips, these swellings have been interpreted as sporangia, but there is as yet no sufficient evidence of this.

There can be no question of the reference of the Orkney specimen to *Pseudosporochnus*, and it can be placed in the one species *P. Krejčii*. This adds another to the types of Middle Devonian plants that are common to the Scottish and Central European Middle Devonian floras.

#### ACKNOWLEDGMENTS.

I am indebted to the Director of the Geological Survey for facilities in studying specimens collected by Dr KIDSTON and now placed in the Kidston Collection. My thanks are also due to my laboratory assistant, Mr ASHBY, who has taken most of the photographs.

\* *Flore Dévonienne de l'étage H. de Barrande*, p. 25, figs. 54-81.

#### EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

##### PLATE I.

##### *Zosterophyllum myretonianum*.

Fig. 1. Tuft of the plant spread out on the surface of the stone, showing the elongated branches springing from a confused basal region. At *x* an example of the type of branching with a backwardly directed branch. Appendages are borne on the distal regions of almost all the erect axes.  $\times \frac{2}{3}$ . (No. 55c.)

Fig. 2. Counterpart of a portion of the preceding specimen, showing the peculiar branching more clearly. Nat. size. (No. 55c, *bis*.)

Fig. 3. Upper portion of the specimen in fig. 1, to show the axes with appendages more clearly. Nat. size. (No. 55c.)

Fig. 4. Lateral branch standing out from relatively main axis before turning up; no recurved branch. Nat. size. (No. 118b.)

Fig. 5. Lateral branch and dichotomy from upper region of an erect axis. Nat. size. (No. 118d.)

Fig. 6. An example of lateral branching with a backwardly directed branch, from the upper region of an erect axis. Nat. size. (No. 118c.)

Fig. 7. Two examples of the branching with backwardly directed branches, giving the appearance of anastomosis. Nat. size. (Powrie Coll., No. 57; Royal Scottish Museum.)

Fig. 8. Two examples of branching with obliquely backwardly directed rhizome-like branches: the vascular strand is traceable throughout. Nat. size. (No. 95.)

Fig. 9. Portion of the preceding specimen, enlarged to show the course of the vascular system more clearly.  $\times 3$ . (No. 95.)

Fig. 10. Portion of a flattened axis dissolved out from the block shown in fig. 1, and macerated. It shows the film derived from the cuticle and the dark linear vascular strand.  $\times 20$ . (No. 640.)

Fig. 11. Tracheides with annular thickening from the edge of the vascular strand of the preceding specimen.  $\times 400$ . (No. 640.)

Fig. 12. Fragment of a vascular strand, not macerated, from a transfer, showing tracheides with annular thickening.  $\times 200$ . (No. 671.)

Fig. 13. Portion of the surface, showing the epidermal cells preserved and seen from the outside.  $\times 100$ . (No. 671.)

Fig. 14. Axis bearing appendages from the same block as fig. 1, photographed on the rock.  $\times 3$ .

Fig. 15. The preceding specimen, transferred to a surface of canada balsam, showing the form and arrangement of the appendages. Full description in the text. Above and to the left is an axis represented by the cuticular film with a displaced vascular strand.  $\times 4$ . (No. 574.)

Fig. 16. Another transfer of an axis with appendages, showing the slender vascular traces given off from the vascular strand of the main axis.  $\times 4$ . (No. 712.)

## PLATE II.

Figs. 17-22. *Zosterophyllum myretonianum*.

Fig. 17. Axis with appendages mostly seen in profile, from Clocksbriggs Quarry. Nat. size. (No. 84.)

Fig. 18. Axis with appendages mostly seen in face view, from Peterden. Nat. size. (Kidston Coll., No. 7199.)

Fig. 19. A portion of the preceding specimen, enlarged to show the reniform appendages more clearly.  $\times 3$ .

Fig. 20. Isolated reniform appendage macerated on the rock and transferred to a cellulose film. It shows the place of union of the stalk and the thickened marginal rim.  $\times 15$ . (No. 685.)

Fig. 21. Portion of axis with a peculiar lateral structure, showing markings of a double series of erect linear-oval bodies.  $\times 3$ . (Kidston Coll., No. 7197.)

Fig. 22. Macerated, transferred cuticle of *Zosterophyllum*, showing markings, the arrangement and appearance of which are suggestive of ill-preserved stomata.  $\times 50$ . (No. 656.)

Figs. 23-31. *Linear Axes and Spore-masses*.

Fig. 23. Linear spore-masses on surface of rock from Balgavies Quarry. Nat. size. (Kidston Coll., No. 7192.)

Fig. 24. Portion of one of the linear spore-masses from the preceding specimen, macerated and mounted in balsam.  $\times 20$ . (No. 584.)

Fig. 25. Edge of a macerated spore-mass, like that in the preceding figure, showing the spores.  $\times 200$ . (No. 583.)

Fig. 26. Transfer of slender, dichotomously branched axes from Balgavies Quarry. The narrow dark incrustation near the lower edge was a linear spore-mass enclosed by a filamentous tissue such as composed the other incrustations.  $\times 3$ . (No. 576.)

Fig. 27. Portion of one of the incrustations in the previous figure to show the branched filamentous tissue.  $\times 100$ . (No. 576.)

Fig. 28. Narrow, branched axes from Clocksbriggs as seen in a transfer.  $\times 20$ . (No. 708.)

Fig. 29. Branch-system of narrow axes from Clocksbriggs.  $\times 3$ . (No. 120b.)

Fig. 30. Branch-system of narrow dichotomous axes, with indications of wider terminal structures, from Clocksbriggs. Nat. size. (No. 51.)

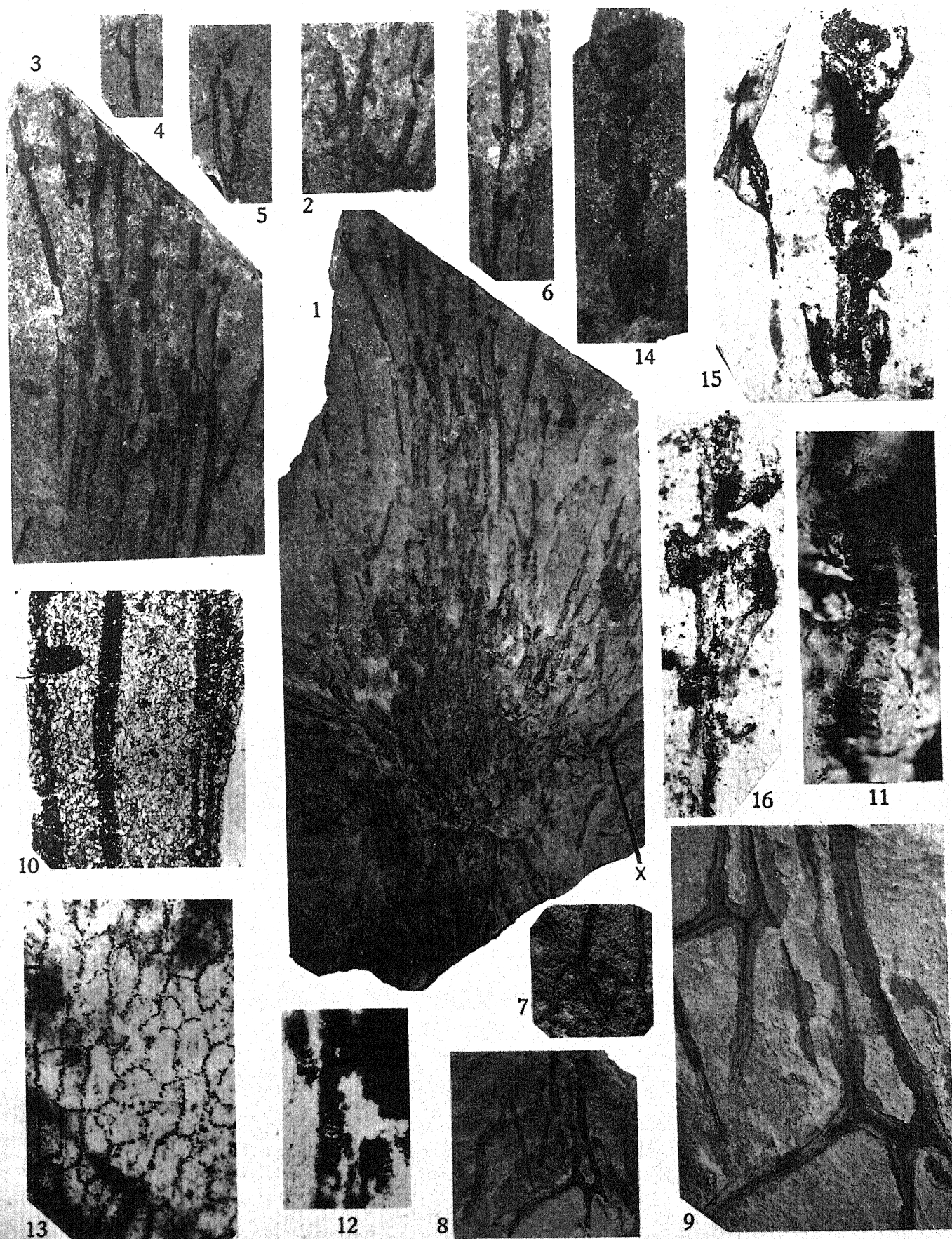
Fig. 31. The preceding specimen enlarged.  $\times 5\frac{1}{2}$ . (No. 51.)

Fig. 32. *Pseudosporochnus Krejčii*.

Fig. 32. Specimen of *Pseudosporochnus* from the Stromness Beds, Orkney.  $\times \frac{1}{3}$ . (Stromness Museum.)





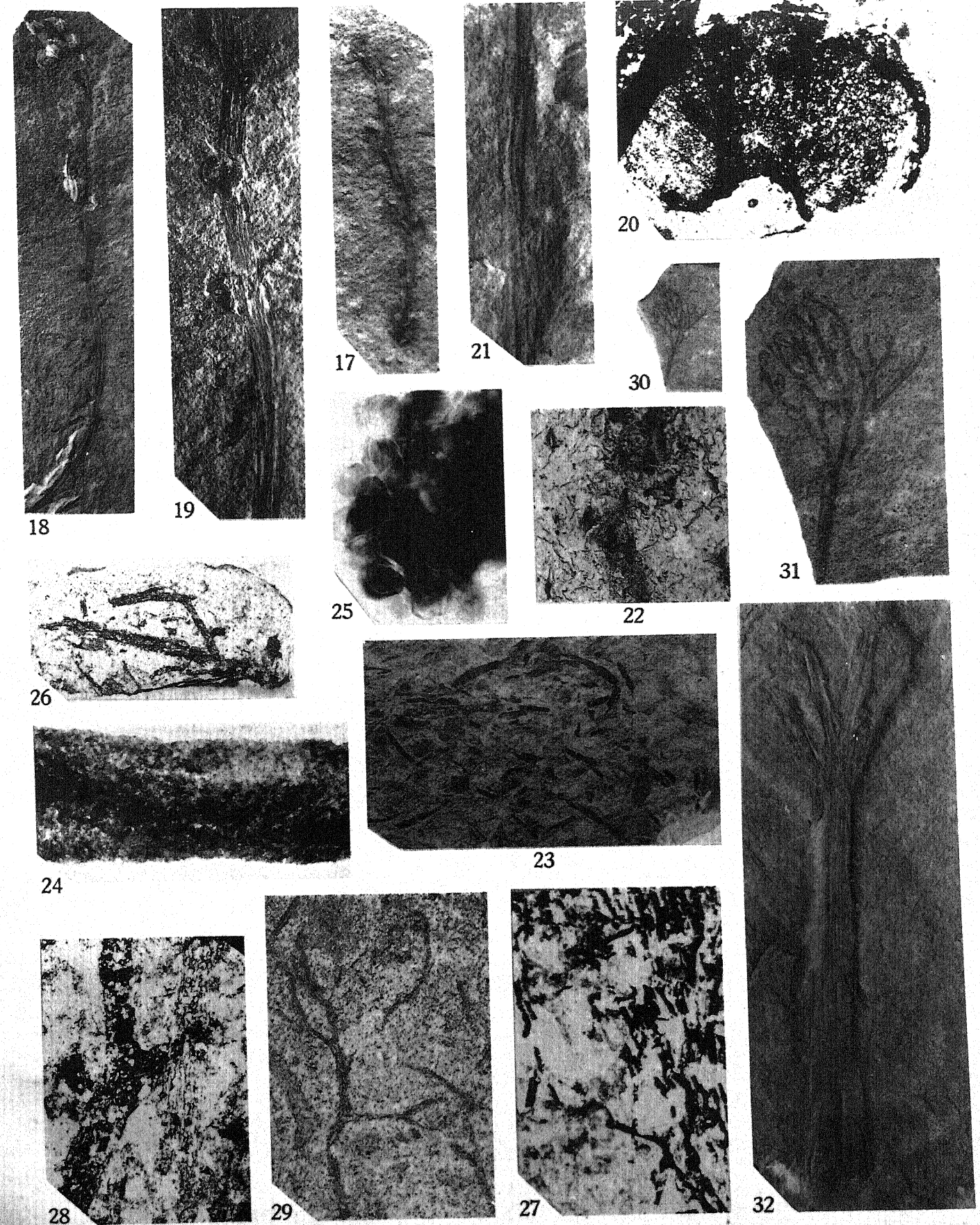


W.H.L. & E.A. photo.

Zinco-ColloTYPE Co., Edinburgh.

*Zosterophyllum myretonianum*.





W.H.L. & E.A. photo.

Zinco-ColloTYPE Co., Edinburgh.

*Zosterophyllum myretonianum* — Incertae sedis — *Pseudosporochnus*

17-22

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XX.—Geology of the Outer Hebrides. Part IV.—South Harris. By Professor T. J. Jehu, M.A., M.D., F.G.S., and R. M. Craig, M.A., B.Sc., F.R.S.E. (With Five Plates and Two Text-Figures.)

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I. INTRODUCTION—PHYSICAL FEATURES.

Harris is supposed to derive its name from the Gaelic “na hardibh,” a designation signifying “the heights.”\* The term is appropriate in that the most mountainous parts of the Long Island lie within its boundaries.

South Harris forms a natural geographical division for it is divided, from North Harris by a narrow neck of land at Tarbert separating the eastern from the western seas. This isthmus is less than half a mile across. In addition to South Harris proper, this memoir deals also with the Isle of Scalpay and neighbouring islets off the north-east coast, the Isle of Taransay on the north-west, and several islands off the south-west coast in the Sound of Harris, of which the principal ones are Ensay, Killegray, Groay, Lingay, and Gilsay.

South Harris is somewhat rectangular in shape and has a south-westward trend from Tarbert to the south of Harris. It is bounded on the north-east by the deep indentations of East and West Loch Tarbert, on the south-east by the Minch, on the south-west by the shallow Sound of Harris, and on the north-west by the Atlantic. Measured along the main trend it is 12 miles in length, with a breadth varying from 6 to 9½ miles. The broadest parts are at the south-west end and near the north-east end. At the extreme north-east end it becomes constricted to the isthmus at Tarbert.

The Isle of Scalpay lies at the north-east entrance of East Loch Tarbert and is separated from the north-east coast of South Harris by a channel nearly 2½ miles broad. It is an undulating rocky island with a very irregular coast-line, and has a maximum length of nearly 2¾ miles, with an extreme breadth of 1¾ miles. A number of smaller islets lie on its inner side in East Loch Tarbert. It is separated from North Harris by the narrow Sound of Scalpay. Scalpay and the neighbouring islets obviously form a continuation of the north-eastern corner of South Harris. The highest elevation on the islet is Ben Scoravaick (341 feet).

\* *The New Statistical Account of Scotland*, 1845, vol. xiv, p. 155.

Taransay, on the north-west coast, is separated from South Harris by a shallow sound only a mile wide at its narrowest part. It trends from north-east to south-west and is a little over 4 miles in length, with a breadth which varies from  $2\frac{1}{2}$  miles to less than  $\frac{1}{4}$  mile. It consists of two unequal parts separated by a low sandy isthmus. The larger north-eastern portion is characterised by bare, rounded hills, the highest being Ben Raah (875 feet). The south-western part, known as Airdvanish, is lower, the greatest elevation amounting to 324 feet, and it is mostly covered by grass and peat.

The isles of the Sound of Harris are low and trend N.W.-S.E. They lie at distances varying from  $1\frac{1}{2}$  miles to 3 miles from the south-west coast of Harris. Ensay is a little over 2 miles long with an extreme breadth of  $\frac{3}{4}$  mile. Killegray is  $2\frac{1}{4}$  miles long, with a greatest breadth of about  $\frac{3}{4}$  mile. The other islets are small and rocky in character. They lie at the south-east entrance of the Sound of Harris.

The high ground forming the backbone of South Harris lies on the north-west and south-west sides and is roughly "L"-shaped, with a projection to the north-west at the base of the "L." Along the greater part of the south-eastern side the ground east of the mountainous ridge forms a rugged uneven slope terminating on the coast of the Minch in cliffs of varying height, and presenting usually a rocky, bare, and desolate surface chequered by numerous small freshwater lochs. The hilly area is traversed by a number of valleys having a N.W.-S.E. trend. Bordering the Sound of Harris an uneven ridge can be traced from Rodil on the south-east to Toe Head on the north-west. It reaches a height of 687 feet south-west of Glen Rodil at Strondeval, and as followed north-westward sinks to 338 feet at Ben Obbe. At Leverburgh it is intersected by the Obbe (an inlet of the sea), to the north-west of which it rises again at Ard an t-Sruith to 200 feet, and again farther north-west at Bideinan to 363 feet, whence it descends almost to sea-level at the neck joining the main part of Harris to the high peninsula terminating in Toe Head. This peninsula is dominated by Chaipaval, which shows twin heights of 1201 feet and 1092 feet respectively, with relatively steep slopes on all sides, but especially on the south-west. North-west of Glen Rodil, Roneval forms a somewhat isolated ridge, attaining an elevation of 506 feet, with a projection to the south-east (Beinn na h-Aire) and another to the north-north-west, including Bosival (over 100 feet) and Mas Garbh (925 feet).

East-north-east of Roneval lies Sletteval (500 feet). The main limb of the "L" increases in elevation and breadth as traced from south-west to north-east. It includes the following hills and mountains: Greaval (922 feet) and Maodal (820 feet), lying parallel to the low ridge bordering the Sound of Harris just where it declines to the isthmus connecting South Harris with the Toe Head promontory; Bleaval (1305 feet), with the subsidiary heights of Mula (847 feet) to the south, and Bolaval (868 feet) to the west; Bulaval (1160 feet), Helsival More (1237 feet), and Helsival Beg (812 feet), An Coileach (1265 feet), Maoladh Mhicearraig (1111 feet); West Stocklett (over 600 feet) and East Stocklett (620 feet), the head of the "L" being formed by the heights of Ben Luskentyre, including from south-east to north-west Uaval More (1166 feet), Ceann Reamhar (1529 feet), Mullach Buidhe (over 1250 feet), and Beinn Dhubh (1654 feet). A strip of low ground varying in breadth intervenes between these heights and the north-west coast-line. This strip is covered by a skin of drift and sand, and usually forms good agricultural land.

An interesting feature in connection with the rocks composing them is the different type of surface which they present. The low ridge parallel to the Sound of Harris is for the greater part of its extent comparatively smooth and covered by grass and heath. Chaipaval, Greaval, Maodal, and Bleaval, with its subsidiary heights, have smoothly rounded outlines

with a covering of peaty soil with grass and heath; the Roneval ridge is grey in colour and is to a large extent capped by blocks of the weathered rock; while the hills from Bulaval to Ben Luskentyre have rather rounded tops showing considerable areas of bare rock and some accumulations of boulders, while at other places they are grassy.

The hilly ridge forming the backbone of South Harris is traversed by a number of well-marked valleys, most of which have a persistent N.W.-S.E. trend. Between the Strondeval-Chaipaval ridge bordering the Sound of Harris and the mass of Roneval at one end and Greaval and Maodal at the other, a distinctive feature is formed by the narrow depression forming Glen Rodil, Glen Strondeval, and Glen Coishletter, and probably continued in the sandy beach which runs out to sea between the Toe Head promontory and Maodal. The well-marked valley in which Loch Langavat lies can be followed from Lingara Bay on the south-east coast to Borvemore on the north-west coast. This depression appears to be continued in the low sandy isthmus which separates the Isle of Taransay into two unequal parts. The heights of Bulaval, Heilisval, An Coileach, and Maoladh Mhicearraig are separated by comparatively high passes having a similar trend, and the last-named hill has a lower pass known as Bealach Teoravat intervening between it and the Stocklett hills. These hills in turn have a valley lying between them and the Luskentyre ridge, occupied in its western part by the River Laxdale, and farther east by a chain of small lochs, the chief of which is Loch Bearasta Mor. The main road from Tarbert to Rodil follows this depression where it traverses the hilly ridge from east to west. The neck of Tarbert, with the depressions formed by the East and West Loch Tarbert on either side, represents a valley having the same general trend. Many of these north-west and south-east valleys and passes coincide with lines of crushing. The Loch Langavat depression is carved out of a group of schistose and granulitic rocks which show crushing at places. The depression farther south along Glen Rodil, Glen Strondeval, the Obbe, and Glen Coishletter lies along the strike of relatively soft gneisses and schists partly of sedimentary origin.

One well-marked valley runs approximately at right angles to those already mentioned, namely, Voumasdale, occupied by a stream (Abhuinn an Uisge) draining Loch Langavat and running into Loch na Maracha, which in turn drains by a small stream into Loch Steisevat and thence by the Obbe into the Sound of Harris.

There are no large streams in South Harris owing to the absence of adequate gathering grounds. Numerous rivulets run south-eastwards from the hilly ground into the Minch and show the same trend as the valleys and passes between the individual heights and ridges. These are obviously consequent streams. The River Laxdale, flowing between the Ben Luskentyre heights and the Stocklett hills, runs north-westwards into the Sound of Taransay, and appears to be an obsequent stream. A few smaller streams of a similar nature drain the north-western slopes of the hills into the western sea. The Horsaclett river draining the south-western slopes of Bleaval and its subsidiary heights is a consequent stream running south-eastwards into Loch na Moracha, where it has been deflected by the stream occupying the valley already mentioned as draining into the Sound of Harris. The stream flowing in Glen Rodil has its source on the southern slopes of Roneval, but it appears likely that at one time the Horsaclett river ran along Glen Strondeval into Glen Rodil. A few streams drain the north-eastern slope of the Roneval ridge and join the consequent streams flowing into the Minch.

The largest loch in South Harris is Loch Langavat lying in one of the main north-west south-east valleys. It is  $2\frac{1}{2}$  miles long and has a breadth of somewhat under half a mile near the middle, but tapers rapidly at both ends. Its surface lies at an elevation of only about



100 feet above sea-level. Beyond both ends smaller lochans are found at slightly higher elevations. It is curious that this loch is not now drained by a stream flowing from its south-eastern end into Strath Leetein, and thence to the Minch as one would expect, but by a stream flowing from the south-western side along Voumasdale. The next in importance are Loch na Moracha and Loch Steisevat. The former is 1 mile long trending from N.N.W. to S.S.E., with a breadth of 100–200 yards, except at its southern end, where it widens from W.N.W. to E.S.E. to a little under half a mile. Loch Steisevat trends from W.N.W. to E.S.E. and has a length of nearly 2 miles, with a breadth varying from  $\frac{1}{4}$  mile to less than 200 yards. The Obbe has a similar trend and a length of  $\frac{3}{4}$  mile, and though now entered by the sea, it obviously represents a drowned freshwater loch. Numerous small lochs are interspersed on the bare and rocky ground between the hills on the north-western side of South Harris and the Minch. These are mostly rock basins occupying hollows in the gneiss, but some of them are partly held up by drift and peat. Loch Stocklett, off Bagh Stocklett, near the head of West Loch Tarbert, is held up by a stormbeach. None of the lochs of South Harris has been sounded.

The south-east coast-line of South Harris, including the Isle of Scalpay, is very irregular, being deeply indented by sea-lochs. The shores are rocky and show considerable variations in height. The indentations of the sea have the same N.E.–S.W. trend as the valleys already described. Their course appears to have been determined by erosion along the strike of the gneiss by joints, and possibly to some extent along the minor N.W.–S.E. line of shearing. They are exposed to the south and do not afford good shelter for shipping. The coast-line facing the Sound of Harris and trending N.W.–S.E. is fairly straight, the only interruptions of any note occurring at the Obbe and at the narrow isthmus composed of sand and drift which almost insulates the Toe Head promontory. A number of small islets border the shore-line between South Harris and the isles of Ensay and Killegray. The north-west coast is not as indented as the south-east coast. It consists of rocky headlands with intervening stretches of sand, the most extensive of which are Traigh an Taoibh Thuath on the inner side of the Toe Head promontory and Traigh Luskentyre at the mouth of the River Laxdale. Some areas of blown sand are found on this coast-line. As usual in the Outer Hebrides deep water occurs close to the south-east coast, while the sea is shallower on the north-west coast and in the Sound of Taransay. The deepest indentations are formed by East and West Loch Tarbert, which almost insulate South Harris. The western loch lies between high mountains that descend by steep declivities to the sea. The slopes of East Loch Tarbert are not as steep, though fairly high cliffs are shown at places. The Sound of Harris is so shallow as to be dangerous for navigation.

While the greater part of South Harris is rocky and bare there are considerable areas of peat in favourable situations, such as in the Loch Langavat valley, in Voumasdale, around Lochs na Moracha and Steisevat. Considerable tracts of peat also occur on the Isle of Scalpay. In some places bordering the southern and western shores the declivities are covered by drift deposits yielding tolerable pasture, and on the north-west coast there are some tracts of machairland. Rodil valley, with its greenish pastures and some trees, presents a pleasant contrast to the more desolate scenery of the greater part of South Harris. The climate is moist and the prevalent winds blow from the south and west. Spells of dry weather are not infrequent in the late spring and early summer, and although wet weather is to be expected for the greater part of the year, rain is more persistent in September, October, and November.

As usual there are no indications of recent raised beaches. The sea-lochs indenting the eastern coast-line owe their origin in part at any rate to submergence. The Obbe on the south-west coast affords an excellent example of a recently drowned freshwater lake.

Peat is seen to pass below high-water mark in some of the inlets. A good example is displayed at Charnish on the north-east coast of Killegray Island. It is obvious that the Sound of Harris and the deep indentations formed by West and East Loch Tarbert represent old consequent valleys which are now covered by the waters of the sea.

## II. PREVIOUS LITERATURE.

MACCULLOCH\* described Harris as being "a country of gneiss." He drew attention to some peculiar types occurring in this area, and added that "something is still left undiscovered, amidst its almost inaccessible deserts, to reward the toils of future geologists." He noted that in Roneval the gneiss loses to some extent the laminar character, "becoming thus scarcely distinguishable from granite." "Hornblende is here abundant, and in the same specimens are numerous large garnets often possessing an imperfect degree of transparency. In some instances the garnet is not separately crystallised, but so equally diffused through the rock as to give the whole a dark crimson blush. Among the veins of granite are found beautiful examples of the graphic variety, of which the felspar is white, translucent, and nacreous, acquiring after exposure an argentine brilliancy."

He identified a ridge of limestone in the Rodil valley and stated that "it lies among the gneiss and is often accompanied by a sort of micaceous schist, the position being irregular, but generally vertical." He compared this limestone to that found in Tiree, and noted that it contains serpentine, grey and watery sahlite, and some dark green coccolite, with some mica and hornblende. He recorded the presence of a band of serpentine on the Isle of Scalpay, traversing the promontory at the eastern end on which the lighthouse stands. The serpentine is said to show considerable variety, some of it having a schistose aspect and fissile structure, while some is more massive, and talc slate is found occasionally on the boundary between the gneiss and the serpentine. Granite veins were observed to traverse the serpentine as well as the gneiss. In the Isle of Taransay he found conspicuous granite veins remarkable for the magnitude and beauty of the crystals of mica which they contain. He observed that trap veins were rather scarce in South Harris, but he noted several in the Isle of Scalpay.

HEDDLE† referred to an interesting rock in the southern part of South Harris which he termed an eclogite. It extends as a ridge from Ben Chaipaval on the west to Roneval on the east, having a length of about 8 miles and a breadth of about 2 miles. It is described by him as an almost non-laminated massive rock consisting "in greatest part of garnet, in less of smaragdite, and in still less of kyanite." He stated that "on rounding to the northward the eastern extremity of this ridge, the hornblendic rock is again met with, its layers laced and bound together by huge granitic dykes. This extends to the northward as a gently undulating country for a distance of some 7 miles, with a breadth of about 4. In no other part of Scotland is such an expanse of utterly barren waste to be met with." He drew attention to a remarkable ridge of serpentine traceable almost across South Harris from south-east to north-west on the north-eastern side of Loch Langavat and beyond both extremities of that loch. This ridge forms a number of eminences above the gneiss, the most prominent of which is Scara Ruadh. With regard to this ridge he observed that "while at the more easterly, the loftier end of the red ridge, the whole rock is a massive perfectly-formed serpentine, as we approach the west, foliaceous flakes of enstatite, or some one of the

\* *A Description of the Western Isles of Scotland*, 1819, vol. i, pp. 163-170.

† *Trans. Roy. Soc. Edin.*, vol. xxviii, pt. ii, 1877-78, pp. 546-549.

minerals which cluster round augite, become visible. Farther west still, where the ridge begins to diminish in height, the hornblendic type of mineral appears as a matted asbestiform actynolite; while at its termination, in the comparatively low Dun of Borge, true unaltered hornblende of the smaragdite type is alone seen—mixed, however, with a concreting felspar."

He was much impressed by the intensely glaciated appearance of this ridge, which shows "terrific gougings 30 and 40 feet in length, and large enough to hold a limb, if not a body; trenches in which a herring boat might lie concealed; and rounded haunches, after the similitude of the hindquarters of an elephant."

In another place HEDDLE \* recorded the presence of sahlite of a grey colour and waxy lustre in the limestone at Rodil. He surmised that the long stretch of Loch Langavat may represent a second, but here washed out limestone bed, but adds that there is no direct evidence of this. Another interesting feature detected by him was the occurrence of a fragmented and reagglutinated rock of singularly jasperine appearance on the north side of the road which passes Loch Bearasta Mor in the Luskentyre valley. He accounted for it by the crushing and recementing of the adjacent rock. The occurrence of a granitic rock in the north-western part of South Harris is referred to as follows: "A rock which doubtless will come to be of economic interest occurs at the western foot of Aird Nishibost. This is a syenitic black mica-granite—apparently a huge vein. It has every property of a first-class building-stone."

JAMES GEIKIE † showed that the Outer Hebrides were traversed by ice that streamed out from Skye and the mainland. "The *mer de glace* was sufficiently deep to fill up the Minch (50 to 100 fathoms in depth) and to drown all but the tops of the highest mountains in its passage outwards to the Atlantic. . . . The islands everywhere bear traces of severe glaciation, the only points which have escaped being those that exceed a height of 1500–1600 feet. The more or less isolated mountains are merely huge *roches moutonnées*." In a map he showed that the ice traversed Harris in a direction from south-east to north-west. He pointed out that the unfossiliferous till is composed of local material with few, if any, erratics derived from Skye and the mainland. Owing to the depth of the Minch close to the east coast, the lower strata of the *mer de glace* would not pass over Harris, but would be deflected to the right and left, and only the upper portion would overflow the land. As an indication of subsidence he states that "in Harris, where alluvial deposits have been undermined and cut back by the sea, 'a rich loam or black moss' is discovered." ‡

In Sir ARCHIBALD GEIKIE's geological map of Scotland the whole of South Harris is depicted in one colour as being made up of Lewisian gneiss with a blue band representing the limestone at Rodil.

### III. GENERAL ACCOUNT OF THE ROCK FORMATIONS.

South Harris and the neighbouring islets appear to be made up of rocks belonging to the Archæan Complex. The only exceptions are dykes belonging to a later age and some glacial and recent deposits (Pl. V).

The Archæan Complex consists of various types of orthogneisses, and in this area there are also present well-marked bands of paragneisses. The orthogneisses of the islets in the Sound of Harris present a close resemblance to the rocks of Pabbay, Berneray, and the northern part of North Uist, and consist for the most part of acid biotite-gneisses with bands of dark hornblende-gneiss and abundant pegmatites. The prevalent strike is N.W.–S.E. with

\* *A Vertebrate Fauna of the Outer Hebrides*, by J. A. HARVEY-BROWN and T. E. BUCKLEY, with notes by Prof. HEDDLE, 1888, pp. 232–235.

† *The Great Ice Age*, 3rd ed., 1894, pp. 82, 156–159.

‡ *Ibid.*, p. 293.



usually a gentle dip to the north-east, but in the smaller islets of the south-east end of the Sound the foliation planes become nearly vertical. Again, along the south-east coast of South Harris, north-east of Finsbay, there is a considerable development of acid and basic gneisses, sometimes granulitic, which bear a close resemblance to the rocks along the eastern side of North Uist. The prevalent strike is again N.W.-S.E. with a dip of varying degree to the N.E., except where the rocks have been affected by a crush zone.

Apart from the rocks above mentioned the types of gneisses found in the area under consideration differ markedly from those occurring in the island farther south. Two well-marked bands of paragneisses associated with various types of orthogneisses were noted, one bordering the Sound of Harris from Rodil to Toe Head, and the other extending across South Harris from the neighbourhood of Finsbay along the Loch Langavat depression to the west coast between Bay Steingie and Borve, and continued probably into the southern part of the Island of Taransay. The paragneisses include crystalline limestones, quartz-schists, quartzose rocks, graphite schists, garnetiferous quartz-schists, garnetiferous sillimanite-gneisses, and garnetiferous kyanite-gneisses. With these are associated hornblende-schists and gneisses, and hornblende-pyroxene rocks which are probably of igneous origin. In the southern band all these rocks have been subjected to intense and sharp folding, and the foliation planes are usually vertical or highly inclined with a well-marked strike from S.E.-N.W. This folding has resulted in the repetition of bands and lenticles of the crystalline limestones and associated rocks. The rocks of the band along the Loch Langavat depression, as seen on the north-west coast of Harris, have the same strike but show gentler dips of the foliation planes, the direction of dip changing as traced northwards from north-east to south-west. The presence of certain fine-grained hornblende-schists is a noteworthy feature in this band. Between the two bands above mentioned lies a belt traversing South Harris from coast to coast, which appears to be made up in large part of an igneous complex bearing intrusive relationship to the rocks of the bands on either side. Towards the south-east at Roneval and Beinn na h-Aire, the intrusive rock is a beautiful anorthosite-gneiss consisting largely of labradorite felspar, but along the margins becoming more gneissic in structure owing to the occurrence of garnets and other dark minerals arranged in linear fashion, and to inclusions probably derived from the country rock. North-west of Voumasdale the prevalent rock has often a massive appearance, and may be described as a gabbro-diorite. In the part of the belt between Roneval and the gabbro-diorite other types make their appearance, such as eclogite, garnet-amphibolite, acid-gneisses, hornblende-gneisses, and garnetiferous hornblende-gneisses. Some of these may belong to the original country rock into which the anorthosite-gneiss and gabbro-diorite were intruded, and some of them may be modifications of the intrusive rocks themselves. Probably belonging to the same period of intrusion are certain ultra-basic bands found in various parts of the area, which have been for the most part converted into serpentines. North of the Loch Langavat band, the greater part of South Harris and of Taransay is made up of a granite-gneiss which sends tongues and bands into the orthogneisses of south-east Harris (Pl. II, fig. 2). This granite-gneiss around the Sound of Taransay is margined by biotite-gneisses and hornblende-gneisses of varying texture, and at places inland similar types are exposed here and there within the granite-gneiss area. Associated with the granite-gneiss and extending to the regions south and east are abundant pegmatites.

The relationships of these various bands to each other are not very clear, but it would appear that the paragneisses and the igneous rocks associated with them are the oldest within the area, and that the anorthosite-gneiss, gabbro-diorite, and some of the associated rocks of that band are intrusive into them. The ultra-basic bands may belong to the same period

of intrusion as the anorthosite-gneiss and gabbro-diorite masses, for at places they are found traversed by pegmatites. The granite-gneiss is obviously later than all the other bands mentioned, and the pegmatites may be regarded as a late phase of the granite-gneiss intrusion. The orthogneisses of the islets in the Sound of Harris and those occurring on the south-east coast north of Finsbay are obviously earlier than the granite-gneiss, but their relationship to the rocks of the other band is obscure.

Along the eastern margin of South Harris and the neighbouring islands there is evidence of crushing, with the formation of mylonites at places, and rarely the occurrence of flinty crush material traversing the rocks in veins. Along this margin a new foliation has sometimes been superinduced on the rocks running from south-west to north-east. The crushed zone has no clearly marked base as in the islands farther south, and it is obvious that the great belt of shearing described in North Uist and elsewhere only touches the south-eastern border of South Harris and Scalpay.

The later dykes include olivine-dolerites, tholeiites, and lamprophyres, and most of them are probably of Tertiary age.

Evidence of glaciation is abundant all over the area, and shows that the region was traversed by ice moving from south-east to north-west.

## 1. THE ARCHÆAN COMPLEX.

### (a) *Gneisses of the Islands in the Sound of Harris.*

The shallow Sound of Harris in the immediate neighbourhood of the south-west coast of Harris is studded by numerous islands, stacks, reefs, and shoals, which trend from N.W.—S.E. in the same direction as the coast. It was found impossible to land on all of these, but the largest, namely, Ensay, Killegray, and Gilsay, were visited, and observations on the others were made from the boat. On these islands the strike of the gneisses is N.W.—S.E. with a gentle dip to the north-east on Ensay and Killegray, but on Gilsay and the neighbouring islets the dip of the foliation plane is much steeper and indeed becomes vertical in the north-western part of Gilsay. The south-eastern part of Gilsay shows marked evidence of crushing and shearing. The rocks there are traversed by veins of flinty crush material and are sometimes reduced to green mylonites. The rocky stack Dun-aarin (93 feet high), lying to the north of Gilsay, is made up of much disturbed gneiss with overfolding from a south-east direction. A great pebble beach traverses the north-western extremity of Gilsay, and among the pebbles occur examples of flinty crush material. Gilsay attains an elevation of 88 feet, and the north-western part of the island is made up of well-foliated biotite-gneisses with some bands of dark hornblende-gneiss.

The acid biotite-gneiss shows predominant quartz and feldspar and is usually medium grained, but contains augen up to  $\frac{1}{4}$  inch in length, indicating that the rock has been reconstructed from a coarser type of similar composition. The feldspathic part is pinkish in hue. Under the microscope this rock shows equal proportions of quartz and feldspar (orthoclase and oligoclase) with subordinate green decomposed biotite associated with epidote. Apatite is also present in fairly large crystals.

Killegray is a flattish island attaining an elevation at one point of 147 feet. Reefs of the harder bands run along the island, giving small escarpments and dip slopes. Acid biotite-gneiss with bands of darker hornblende-gneiss constitute the rocks. Pegmatites are common, especially at the north-west end, and run with the strike and dip of the gneisses. Near the west end on the south-west coast there are some big pegmatites with feldspars over a foot

in length and 6 to 8 inches in breadth. Some of these pegmatites form a striking feature in that they weather white. The acid-gneiss is a streaky quartzo-felspathic rock with biotite, and shows a large augen of felspar and drawn-out quartz in hand-specimens. Under the microscope abundant quartz is seen with about equal amounts of orthoclase and oligoclase, sparing biotite, and a little apatite. The darker bands of hornblendic gneiss contain biotite as well as hornblende along with some quartz and a felspar (oligoclase-andesine). Other examples of the dark bands are well-foliated hornblende-gneisses, containing, however, a little biotite, quartz, andesine, with granular sphene, apatite, and iron-ores as accessories.

Ensay is again a low island with an extreme elevation of 162 feet. The prevailing rocks resemble those of Killegray. In addition, there occur some more peculiar types. For instance, at Manish Point a dark friable schistose band is found resembling some of the schistose types described in the northern part of North Uist. The bulk of the rock consists of hornblende with abundant though subordinate bronzy biotite and a small proportion of plagioclase, and some iron-ores. At the north-west corner of Ensay, south-west of Rudha nan Sgarbh, the prevalent grey gneiss is interbanded with some fine dark hornblende-schist, and also contains nodules, lenticles, and irregular bands of a fine greenish rock. The grey gneiss has a mottled appearance and appears to be granulitic. Under the microscope it is seen to consist of abundant quartz and oligoclase-andesine with hornblende and biotite. Iron-ores and apatite occur sparingly as accessories. The lenticles and nodules of greenish rock appear to consist almost entirely of a pale green amphibole, having the form of needles with which is associated, however, a small proportion of brown biotite.

For the most part, the rocks of these islands resemble closely in texture and composition the rocks of Pabbay, Berneray, and the northern part of North Uist. With the exception perhaps of those described at the north-west corner of Ensay, they differ markedly from the types forming the south-western part of South Harris.

The crushed rock at the south-eastern end of Gilsay and on Dun-aarin appear to belong to the sheared belt occurring on the eastern side of the islands of the Outer Hebrides described in former memoirs.

(b) *Paragneisses and Associated Rocks bordering the Sound of Harris from Rodil to Toe Head.*

The rocks forming this south-western part of South Harris are interesting in that they include many types of sedimentary origin (paragneisses), with which are associated, however, types of igneous origin (orthogneisses), and some the original nature of which is doubtful. These rocks occupy a somewhat narrow belt with the breadth usually of about a mile, which lies to the south-west of Beinn na h'Aire, Roneval, Greaval, and Maodal. Within this belt lie the well-marked valleys of Rodil, Glen Strondeval, the Obbe, and Loch Steisevat, Glen Coishletter, and the depression farther north-west through which the main road runs to the west coast. South-west of these valleys is a low but well-marked ridge running parallel with the Sound and including Strondeval, Beinn Obbe, Ard an t-Sruith, and Bideinan. The north-western extremity is formed by the heights of Chaipaval and Toe Head (Pl. V).

*Paragneisses.*—The rocks of this belt include crystalline limestones, graphite-schists, quartzose rocks, quartz-schists, garnetiferous quartz-schists, garnetiferous sillimanite-gneisses, and garnetiferous kyanite-gneisses, all of which are probably of sedimentary origin. These and the associated orthogneisses have been subjected to intense and sharp folding, and the foliation planes are usually vertical or nearly so, with a well-marked strike from south-south-



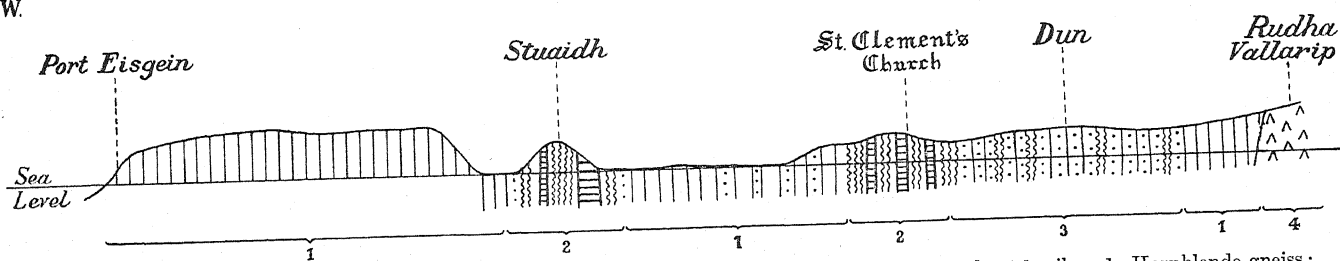
east to north-north-west (text-fig. 1). North-west of the Obbe and on Toe Head the dip is steep to the north-east.

The best exposures of the crystalline limestones are in the neighbourhood of Rodil. There appear to be two main series of outcrops. The southernmost is seen on the north-east side of Stuaidh, a promontory at the head of Loch Rodil. This is the broadest outcrop in the district, with a north-west strike and a vertical dip, and having a breadth of about 100 feet at the widest part. It is lenticular in form and inland disappears under a grassy slope. The outcrop is not continuous, but occurs as isolated knobs and lenticular ridges projecting through grassy ground. It weathers yellow and shows a rough surface, due to lumps of varying sizes projecting from the rock surface. These lumps are usually about the size of one's fist, but are sometimes larger. The limestone is here wrapped round and partly interbanded with a reddish, rusty weathering, highly-garnetiferous rock.

The other series of outcrops can be traced from the Isle of Vallay through the St Clement's Church ridge on to Glen Rodil. It appears again on the south-west side of Glen Strondeval and can be followed almost to Loch Obbe. It probably extends under the

E.

W.



TEXT-FIG. 1.—Diagrammatic section from Port Eisgein to near Rudha Vallarip. Length of section about 1 mile. 1. Hornblende-gneiss; hornblende-biotite-gneiss; hornblende-pyroxene-gneiss, with occasional bands of garnetiferous mica-schist. 2. Crystalline limestones, with ferruginous quartz-biotite-schist, sometimes graphitic. 3. Grey garnetiferous gneiss with lenticles of ferruginous biotite-graphite-schist. 4. Crushed anorthosite-gneiss.

depression of the Obbe; and at the north-west end of this loch a grassy hollow may indicate its concealed continuation in that direction.

In the Isle of Valley at least two bands of limestone are exposed on the coast, both on the south-east and north-west sides, and these bands are probably continuous across the islet though concealed under grass. They are interbanded with a fine grey highly-ochreous and graphite-bearing rock, and with a reddish highly-garnetiferous rock and grey garnetiferous gneiss. On the south-east coast these rocks are at places crushed and mashed together. The bands are vertical and strike north-north-west. They appear again at the south-east end of St Clement's Church ridge and outcrop in several bands along this ridge. The best exposure is seen at the north-west end of the ridge, where a small quarry has recently been opened. At least three bands of limestone outcrop in the St Clement's ridge, alternating with other types in more or less vertical strips with a strike a little west of north. These bands appear to be isoclinally folded. The limestone can be traced in intermittent fashion in a north-west direction. A lenticle crops out on the slope of Druim Skeilibreck overlooking the grassy ground, lying south-west of the road bounded on both sides by a highly-garnetiferous reddish ochreous weathering rock. Several bands of the limestone crop out to the north-east of the road and can be followed in an intermittent fashion to the region between Loch Ossigary and the road leading to Leverburgh. Between the road and the south-east end of this loch four bands of limestone were noted, separated from each other by grey gneiss and the ochreous reddish weathering highly-garnetiferous rock. One of these bands is seen

on the south-west margin of the loch, and it is quite possible that still other bands pass under the loch.

Outcrops of the limestone are last seen in Glen Rodil between the road and Toan, but it appears likely that limestone is concealed farther to the north-west under the green verdure.

The next outcrop in a N.N.W. direction appears on the slope between Beinn Obbe and Glen Strondeval passing through Loch Cistevat, with a reddish highly-garnetiferous rock on either side. This can be followed in an interrupted fashion as already mentioned almost to the south-eastern extremity of the Obbe. It is obvious that the limestone appears in lenticular outcrops of varying thickness, and that it is interbanded with various types of altered sediments, and occasionally with altered igneous rocks. In the Isle of Vallay and at the north-eastern corner of St Clement's ridge it is in contact with a fine grey ochreous graphite-bearing rock. At the small quarry already mentioned it is bordered by a light micaceous calc-silicate rock with a quartzose band on either side. Farther to the north-west and in some parts of the St Clement's ridge a constant companion is the reddish highly-garnetiferous and ochreous weathering rock. The outcrops of the limestone are usually marked by good grass in contrast with the heath which occurs on the associated rocks.

The typical limestone (Pl. I, fig. 1), as seen in the St Clement's Church quarry, is a grey-mottled rock weathering with a rough surface and marked by conspicuous white ovoid masses of diopside up to 6 inches in greatest diameter. Under the microscope (Pl. III, fig. 1) it shows abundant rounded grains of forsterite partly serpentinised, a feebly pleochroic phlogopite, clear colourless diopside, and occasionally a little graphite, all these minerals being set in a matrix of granular calcite in which also occur occasional rhombs of dolomite. Graphite in glistening scales is most abundant near the edge of the limestone, where there also occur narrow strips of matted calc-silicates and talc. Thin veins of a greenish-yellow serpentine also traverse the rock. The white nodules, which vary in size from a fraction of an inch up to 6 inches in diameter, are often surrounded by a thin, dark border of serpentinous material. These lumps, which may represent original nodules in a dolomitic limestone, consist for the most part of a white or nearly colourless diopside along with which there may be a small proportion of forsterite and calcite. The limestone and the enclosed nodules contain scattered particles of pyrite. The limestone at Stuaidh shows the same characters and is more graphitic and less pure on the edges than in the centre.

The lenticular nature of the limestone may be due to pressure and movement, the limestone being more plastic than the siliceous sediments with which it is immediately associated. Thus at Stuaidh on the north side of the exposure the limestone contains fragments of the adjacent rock (a fine-grained quartzose rock containing biotite), around which it seems to have flowed. At some of the smaller outcrops, as for instance that at the piers at Rodil, the limestone occurs in thin strips alternating with a grey pyritous rock, and shows abundant amber-coloured phlogopite.

Immediately in contact with the limestone at some of the outcrops, as for instance in the small quarry at St Clement's Church, is a grey granulitic gneiss with abundant graphite, colourless diopside, much granular sphene, along with a cloudy acid plagioclase. A coarse quartzose band is found on either side of the quarry, and under the microscope this rock is seen to be made up of coarse quartz grains with a little microcline and some carbonate in veins.

A common associate of the limestone, as for instance in Vallay Isle and north-east of St Clement's Church, is a hard fine-grained grey rock weathering with a marked rusty surface (Pl. III, fig. 2). About half of the rock consists of quartz in rounded and irregular grains, some of them compound. These are set in a groundmass which is mostly cloudy, represent-

ing probably decomposed felspar, but it contains also small crystals of an acid plagioclase probably of secondary origin. There is abundant reddish-brown biotite, a few grains of nearly colourless garnet, flakes of graphite, and disseminated particles of brassy sulphide, to the oxidation of which the rusty appearance of the weathered rock appears to be due. Parallel lines of fracture traverse the rock, and the mica and graphite have been distorted. In addition to its association with outcrops of the limestone in the Rodil region, at least six small lenticular outcrops of this type of rock were noted on the Rodil-Finsbay road north of St Clement's Church to a point about a quarter of a mile north-east of B.M. (Bench Mark) 174.2. Some of these lenticles have been quarried in search for iron, and they occur amongst more acid and less graphitic garnetiferous gneisses. A specimen from a small quarry by the roadside shows the groundmass of cloudy feldspathic material in which a few crystals of acid plagioclase are visible, a few rounded irregular grains of quartz, brown biotite, graphite, and grains of pyrite. Somewhat similar types are more quartzose and contain garnets.

A rock weathering in the same manner, but coarser in grain, is well seen just north of the piers of Rodil (Pl. III, fig. 3). It shows rounded and irregular quartz grains, some compound, making up two-thirds of the rock, elastic grains of microcline and plagioclase containing blebs of quartz, some cloudy sericitised feldspathic material, brown biotite, and sparingly disseminated pyrite. This rock appears originally to have been an impure sandstone.

North-west of the Slip, which is situated to the south-west of Rodil Hotel, another rock of similar composition is seen which is made up of rounded grains of quartz and plagioclase (oligoclase) in equal parts, with abundant biotite with which is associated a fibrous mineral, probably sillimanite. This rock is so highly garnetiferous as to have a reddish hue in the field.

This type of rock, so highly garnetiferous that it shows a reddish blush in hand-specimens and in the field, is very abundant along this belt, being frequently seen as a companion of the limestone on either side, and also outcropping where the limestone itself is not visible. Bands of it can be followed from the Rodil region to north-west of the Obbe. It varies considerably in coarseness. An example from the St Clement's Church ridge as seen under the microscope shows numerous large garnets, abundant red-brown mica, along with quartz, plagioclase, and sericitised material. The garnets are traversed by numerous fracture lines and contain minute clear, rod-like inclusions.

A very siliceous band is seen on the east side of the fork of the road east of St Clement's Church. In hand-specimens it is a finely-banded quartzose rock. Under the microscope it is seen to be made up almost entirely of equal-sized subangular quartz grains. A few clear crystals of oligoclase also occur and interstitially there is a very small amount of sericitised feldspathic material. Several small grains of hornblende are also seen, but the most important constituent after the quartz is biotite, which occurs in small light brown flakes. This rock might be described as a micaceous quartzite. A somewhat similar rock with parallel biotites is associated with and enclosed in the limestone at Stuaiddh.

The rocks above described, namely, the crystalline limestones, quartzose rocks, graphite schists, garnet-quartz schists, both fine and coarse in grain, are all well displayed in the neighbourhood of Rodil. Nearer the Roneval ridge other types are found. For instance, 150 yards north-west of Mullach an Struigha, on the steep south-west slope of Beinn na h-Aire, a light-coloured siliceous gneiss occurs, associated with banded hornblendic rocks (described subsequently). Under the microscope about two-thirds of the rock is seen to be composed of quartz in irregular grains. Felspar occurs in groups of granules often showing minute



intergrowth with quartz; it is cloudy from inclusions and includes microcline and an acid plagioclase. Quartz and felspar make up the bulk of the rock. It also contains garnets in irregular grains and biotite and hornblende, with apatite and iron-ores as accessories.

Similar siliceous garnetiferous gneisses are seen on the right bank of Abhuinn Easan Chais, and again forming the low ridge just east of the ravine in the Abhuinn Grimsdale. Both these localities lie about  $\frac{1}{4}$  mile north of the Post Office at Obbe.

Near the same locality, but exposed in the small ravine in the Abhuinn Grimsdale near a small fault, is a quartzose rock closely resembling those seen near Rodil. It is made up almost entirely of quartz in rather large, interlocking grains. Cloudy sericitised and rounded areas of felspar occur sparingly. In one specimen garnet occurs chloritised along cracks, and also some green decomposed biotite and traces of iron-ore with granules of apatite. The rock also contains disseminated granules of pyrite.

At Obbe (Leverburgh) bands are seen of a very beautiful quartzose rock, showing in hand-specimens abundant brown garnet and reddish-brown biotite. These have the usual N.W.-S.E. strike and can be traced in a south-easterly direction to Ben Obbe and in a north-easterly direction to the Toe Head peninsula. The rock varies considerably in texture, being sometimes fine and sometimes very coarse, with garnets reaching a quarter of an inch in diameter. An average specimen contains more than two-thirds quartz occurring in large irregular grains, and also in fine-grained granulitic areas associated with felspar, with which it is often intergrown on a microscopic scale. The felspar includes oligoclase and probably albite. Certain lenticular areas are marked by the occurrence of garnet associated with clusters of red-brown biotite. Generally associated with the biotite, but occurring also to some extent in the quartzo-felspathic parts, are radiating groups of sillimanite (Pl. III, fig. 4). Iron-ores occur very sparingly, and there may also be present minute flakes of graphite. In specimens where garnet and biotite are plentiful, sillimanite is correspondingly abundant.

On the Chaipaval ridge in the Toe Head peninsula the rock is somewhat similar in appearance in hand-specimens, but rather more gneissic in character. It contains conspicuous garnets up to an inch in diameter and short blue blades of kyanite (Pl. III, fig. 5). The garnet and kyanite are not uniformly disseminated through the rock, but tend to occur in lenticular patches. The groundmass of the rock, and indeed the bulk of the rock, is a mosaic of interlocking irregular quartz grains, with which are associated a quite subordinate amount of felspar. The quartz mosaic appears to have been formed by the granulitisation through movement of larger areas of quartz, as shown by the drawing out of the quartz grains and by the prevalence of strain shadows. The felspar is so strained that its identification is difficult, but it appears to include microcline and oligoclase. In this quartzose groundmass are numerous large garnets cracked, drawn out, and sometimes showing anomalous double refraction. In one of them brown biotite has developed along cracks. Occasionally, too, the garnet surrounds quartz and is crowded with minute clear, rod-like bodies. Associated with the garnet is abundant red-brown biotite, and throughout the mass, but mainly beside the garnet and biotite, are prisms up to one-eighth of an inch in length of blue kyanite. The kyanite crystals which sometimes show twinning are broken or bent. In the finest grained parts of the groundmass sillimanite occurs. Small grains of deep brown rutile are also present and grains which may be corundum. It is clear that after the formation of the garnet and kyanite the rock was subjected to pressure but not to extensive shearing. Part of the biotite, however, especially that occurring in cracks in the garnet, appears to be later than the crushing.

Farther north-west on the hillside above Bretasker the typical rock is a siliceous grey gneiss of finer grain than that last described, in which garnet is visible in hand-specimen.

About half the rock consists of quartz in elongated ragged form and in drawn-out granulitised lenticles. Perthitic orthoclase with inclusions occurs in large deformed plates, and an acid plagioclase also in smaller plates, and again to a limited extent with the granulitised quartz. There is abundant red-brown biotite, a nearly colourless garnet much strained and traversed by roughly parallel cracks in which biotite has developed. Bent and broken blades of kyanite also occur with a few grains of deep brown rutile and another mineral which may be corundum. As in the previous type the rock has been crushed but not sheared since the formation of the chief minerals.

At the Geo Mor, Toe Head, the typical rock is a grey granulitic gneiss showing garnets which are larger than the groundmass in which they lie, as seen in hand-specimens. This rock contains about equal parts of quartz and plagioclase felspar (andesine). There is abundant brown biotite, large clear garnets, cracked and veined with biotite, ilmenite drawn out and altering to sphene, and some apatite.

Among these altered sediments rocks which have probably been arenaceous greatly predominate. Some have been very pure sandstone, others have contained varying amounts of impurity, mainly felspathic material. The sediments appear to have been derived from an area of acid rocks.

*Igneous Rocks associated with the Sediments in the Belt bordering the Sound of Harris.*—Interbanded with the sediments, especially in the south-eastern part of the belt, there occur hornblendic or pyroxenic gneisses, often garnetiferous (text-fig. 1). They are well seen in association with the sediments at Stuaidh and on the St Clement's Church ridge and elsewhere, and they also form definite belts north-east and south-west of the sediments. Thus in the Rodil district a triangular area of these rocks lies between the altered sediments and the rocks to the north-east. They are prominently developed on the Renish Point promontory and can be followed bordering the coast to the north-west. In the field these rocks are crumpled and show light and dark streaks. They are usually garnetiferous, the garnets sometimes occurring in clusters or well-defined bands, and at others sporadically scattered through the rock. A specimen taken from the St Clement's Church ridge when seen under the microscope shows quartz, andesine, abundant yellow hornblende often enclosing a nearly colourless monoclinic pyroxene (Pl. III, fig. 6). Garnets are abundant and scattered iron-ores are present. The rock has a coarsely granulitic texture. At Stuaidh a rock of somewhat similar texture, but somewhat crushed, contains abundant hornblende with a little biotite, colourless enstatite, with numerous linear rod-like inclusions, garnets surrounded by a hornblende-quartz mosaic, abundant iron-ores, and large apatites. The rock making up Renish Point is dark grey in colour and granulitic. It consists of quartz, andesine, biotite, hornblende, a light green pyroxene, apatite, and iron-ores. On the south coast of Vallay Isle a crushed grey granulitic gneiss shows yellow-brown hornblende in a groundmass of decomposed plagioclase, crushed garnets, and scattered iron-ores. A granulitic gneiss from the south shore of Carminish, south of Obbe, contains quartz and andesine partly in plates and partly in finely-granulitised areas, and also large plates of green monoclinic pyroxene edged with and partly intergrown with hornblende. There is also abundant biotite, while iron-ores and apatite occur sparingly.

A well-foliated rock on the shore of the Sound of Stromay resembles the one last described in the amount of quartz and the nature of the felspar, but contains clustered hornblende and biotite without pyroxene.

Between the altered sediments and the anorthosite of Beinn na h-Aire some of the bands are very dark in colour. An example taken from a point 250 yards south of the south-west

cairn on Beinn na h-Aire when examined under the microscope is seen to consist largely of a green monoclinic pyroxene with a little hornblende, which occurs partly as separate crystals and partly in intergrowth with the pyroxene. Associated with the pyroxene crystals are rounded fresh garnets, which are generally surrounded by a rim of varying width marked by hornblende rods arranged at right angles to the garnets and intergrown with felspar. Iron-ores occur in scattered crystals and also in strings forming the boundaries of crystals or the quartz hornblende rim surrounding the garnets.

Another band in the paragneisses seen at the north-west end of Loch Ossigary is a remarkably fresh rock consisting mainly of a pleochroic feriferous hypersthene, a little monoclinic pyroxene, and some green hornblende. A somewhat similar rock occurs at Toan at the head of the same loch.

Most of the rocks just described possibly represent metamorphosed lava flows or metamorphosed tuffs. Into these there have been intrusions of basic material now represented by lenticles and irregular bands of hornblende-gneisses and schists.

On the north-east side of the Chaipaval ridge, especially at and near Sgeir Leomadal, rocks of a different character to the altered sediments described as occurring on that ridge are seen. Unlike the kyanite rocks of the ridge they are more massive and show imperfect foliation and are more regularly jointed. Generally they are of darker colour. Under the microscope they have the texture of an igneous rock. They contain quartz in irregular grains subordinate in amount to a well-twinned plagioclase-felspar (andesine), rather abundant pale green monoclinic pyroxene, brown biotite, green hornblende sometimes with a core of pyroxene, abundant garnet, with some apatite and disseminated iron-ore. Other examples taken from the same neighbourhood show similar characters but vary in detail. It is to be noted that these are not like the dark hornblendic gneisses and schists already referred to, but have a distinctly igneous texture and structure. They resemble the prevalent rock in the neighbourhood of Scarastavore, which will be described subsequently.

It may be mentioned that quite recently a narrow band of ultra-basic rock has been exposed immediately south-west of the St Clement's Church ridge.

(c) *The Anorthosite-gneiss of Beinn na h-Aire and Roneval.*

On the north-east boundary of the paragneisses and associated rocks of the Rodil area occurs an interesting mass, which is mainly a labradorite rock or anorthosite-gneiss. It forms the greater part of Beinn na h-Aire and Roneval and is wedge-shaped, the base of the wedge extending along the south-east coast between Rudha Vallarip and Lingara Bay. The mass narrows to the north-west, terminating on the slope near the north-east corner of Loch Steisevat. At the base of the wedge bordering the coast-line this rock and its associates are markedly crushed (Pl. V).

The mass appears to have intrusive relationships to the paragneisses and associated rocks lying to the south-west. This is inferred on the following grounds: (1) the south-west boundary of the mass runs somewhat obliquely to the strike of the Rodil group of rocks; (2) different members of the Rodil group are seen in contact with the mass or occur within a few yards of it. At Mullach an Stuigha the anorthosite mass is in contact with light and dark hornblendic and hornblende-pyroxene rocks, which are interbanded with the Rodil paragneisses. Again north-west of Mullach an Stuigha the mass is seen to lie within a few feet of an acid-quartzose-gneiss, being separated from it by one of the later dykes. Still farther to the north-west, but south-east of the stream which comes down in the hollow between Beinn na h-Aire and Roneval, the margin is involved with an acid pegmatite, both



the anorthosite and the pegmatite showing evidence of crushing. North-west of the stream just referred to the anorthosite forms the steep part of the south-west slope of Roneval, acid-gneiss occasionally appearing near it, but being more often concealed. Between Bo-rhea and a stream named Abhuinn Easan Chais the actual junction is not visible, but acid-gneiss sometimes garnetiferous crops out occasionally between the anorthosite and the stream. Still farther to the north-west in a little ravine in the Abhuinn Grimsdale the anorthosite appears within a short distance of a pyritised siliceous schist of a type common in the Rodil group. Here, however, there is evidence of faulting.

The north-east boundary from the Rodil-Finsbay road runs near the course of the Abhuinn Collam and between it and the Sletteval ridge, which is conspicuous for its large pegmatites; thence it can be followed from the south-east to the north-west wall of Coire Roneval, and from there down the long slope to near Loch Steisevat.

The rocks along the north-east boundary, dealt with in a later section, consist of coarse and fine hornblende-gneisses, granulitic hornblende-biotite-gneisses, with others more acid in composition. All of these rocks are frequently garnetiferous. Except at Coire Roneval, however, the actual junction is concealed. At Coire Roneval and again on the south-west side the boundaries of the anorthosite mass appear to be vertical.

The anorthosite appears to contain inclusions of the adjacent rocks. Thus from near Rudha Vallarip to Lingara Bay numerous inclusions of varying sizes occur of a dark hornblende sometimes garnetiferous, which closely resembles a type of rock well seen on the coast north-east of Lingara Bay. Again on Roneval near the top of the cliff of Coire Roneval several lenticles 3 feet or more in length are seen enclosed in the anorthosite. The lenticles appear to be a garnet-pyroxene rock, which is identical in structure and composition with a component of the gneisses of Beinn Tharsuinn.

The anorthosite attracts attention at once in the field by reason of its predominantly light or sometimes dark reddish colour, and because it weathers differently from all the other rocks with which it is associated. Where not crushed its outcrop is invariably marked by a covering of angular fragments often of great size, well seen on the summit of Roneval (Pl. I, fig. 2).

In the field the rock shows a streaky imperfect foliation, having the usual S.E.-N.W. trend, but this appearance of foliation is much emphasised by the occurrence of small lenticles and narrow bands of darker minerals which have the same trend (Pl. I, fig. 3). These darker lenticles and bands are much commoner along the south and north margins than in the centre, and together they form but a small part of the mass, which is predominantly white or light grey in colour.

In hand-specimens the typical rock has a thin white crust and looks like a crystalline limestone, but on a freshly broken surface the felspar making up the bulk of the rock is often clear and glassy.

Some typical examples from this rock-mass as seen under the microscope may be described. A specimen from a point about 400 yards west of the top of Roneval is a beautiful white, even-grained rock, weathering with an opaque white crust, but on a fresh surface showing clear fresh felspar. It consists almost entirely of equi-dimensional grains of labradorite-felspar (Pl. IV, fig. 1). The other constituents, insignificant in amount as compared with the felspar, are irregular granules of sphene and small scattered crystals of hornblende and irregular grains of epidote.

Another example from the small quarry on the roadside south of Abhuinn Collam consists mainly of labradorite-felspar, which shows numerous minute, black, rod-like inclusions. The other constituents are small crystals of epidote, generally cracked and broken and some-

times reduced to powder. Along with the epidote are occasional flakes of a nearly colourless micaceous mineral. This specimen, taken from near the area of crush, shows obvious signs of disturbance. The lamellæ are often bent and broken, and around the edges of the grains a rim of granulitised material often occurs.

A sample taken from near the edge of the mass on the steep south-west slope of Beinn na h-Aire is fine-grained and shows granulitic structure. It consists mainly of granular labradorite, some of which is untwinned. Crystals of hornblende are scattered irregularly through the mass. Some granules of epidote also occur and probably also scapolite.

Both light and dark portions of the rock are often garnetiferous, especially near the summit of Roneval and on its western slope.

A specimen from the south-west end of Hacklett, near the western end of the mass, shows the usual equi-dimensional grains of labradorite making up the bulk of the rock, but in addition grains of garnet are scattered evenly through the mass and along with the garnet are flakes and granules of hornblende.

The dark parts of the rock occur as mentioned either in small lenticles drawn out in a S.E.-N.W. direction or as narrow bands having the same trend. These dark patches and bands are frequently garnetiferous, more often so than the light parts. They appear to represent segregations of the dark mineral.

An example of one of these dark bands from the north-east side of Beinn na h-Aire (Pl. IV, fig. 2) is coarse-grained, and consists of hornblende and pyroxene, the pyroxene often occurring as a core to the hornblende. Around these groups of dark minerals are rows of granules of garnet, which in turn are surrounded by a border of minute hornblende rods standing roughly at right angles to the boundary and in intimate intergrowth with a clear colourless mineral which appears to be untwinned felspar.

The dark bands are often fine-grained and granulitic in structure. A typical example from near the south-west Survey Beacon on Beinn na h-Aire is made up of a fine-grained aggregate of hornblende, pyroxene, epidote, and iron-ore. The hornblende often contains blebs of felspar, and occasionally the hornblende and felspar form a granular aggregate.

Anorthosites appear to be rare in Britain, but an example has been noticed near Portsoy by Dr HEDDLE,\* and described recently by Dr READ.

(d) *The Gabbro-diorite and Associated Rocks of Bleaval, Mula, Greaval, Beinn Tharsuinn, Mas Garbh, and Sletteval.*

The hilly ground north-west and north-east of Roneval, but south of the Loch Langavat valley is made up of gneissic rocks, generally dark in colour and often garnetiferous. North-west of Voumasdale these rocks are on the whole uniform in character, but to the south-east they become more banded, more varied. Throughout the belt, however, they weather uniformly, showing smooth and rounded hills largely covered by grass and peat.

North-west of Voumasdale the prevalent rock is dark grey in colour and often massive in appearance, consisting of quartz to a sparing extent, plagioclase-felspar, hornblende, biotite, and usually garnet. In the field the rock generally shows a faintly developed north-north-west foliation and exhibits signs of granulitisation. This is the type of rock to which the name gabbro-diorite is applied.

South-east of Voumasdale the gabbro-diorite is much less abundant, being largely replaced by other types such as eclogite and garnet-amphibolite (Beinn Tharsuinn), acid bands

\* M. F. HEDDLE, *Trans. Roy. Soc. Edin.*, vol. xxviii, 1879, p. 252; "The Geology of the Country around Banff, Huntly, and Turriff," *Mem. Geol. Surv.*, 1923, p. 97.

(near Coire Roneval), or hornblende-gneisses and garnetiferous hornblende-gneisses (Mas Garbh, Bosival, and Sletteval).

The nature of the junction between the rocks of this part of the belt and the rocks of the neighbouring belt is not clearly displayed in the field. Inland no clear junctions were observed. On the shore at Bay Steingie on the north-west coast the rock referred to as gabbro-diorite is seen within a few feet of fine-grained hornblende-biotite-schists. The actual junction has been cut to beach-level by the sea, but it is possible to see that both rocks have been subjected to a common movement, fine hornblende-schists with crushed phacoids of the gabbro-diorite being partly concealed by beach material.

A few examples of the gabbro-diorite from the north-west area may be described. The rock at Sgier Liath is dark grey, medium grained, massive, and well jointed, showing a faint foliation in the field, but not in hand-specimen. It contains occasionally short irregular veins of hornblende (probably segregations) and occasional strings of garnets (Pl. I, fig. 4). Under the microscope it shows quartz in small amount, abundant plagioclase (andesine), abundant green hornblende, brown biotite subordinate to hornblende, garnets cracked and sometimes veined with biotite, iron-ores, and apatite.

Another example from the same locality but somewhat farther north is similar in hand-specimen to that last described, but shows under the microscope more evidence of granulitisation. It consists of scattered groups of hornblende and biotite, the latter in small flakes, in a granulitic groundmass of abundant andesine with a little quartz. Small garnets, apatite, and occasional granules of sphene are also present.

A specimen from near the margin at Bay Steingie (Pl. IV, fig. 3) is a massive dark grey medium-grained rock consisting of quartz in small irregular grains, abundant plagioclase, abundant dark green hornblende in irregular sometimes sieve-like plates, irregular flakes, and groups of flakes of biotite, iron-ores, and apatite. The hornblende sometimes has a core of pyroxene.

Inland from the coast the rock maintains the characters described above, the rock of Druim na Caorach, Bleaval, Mula, Meaval, Bolaval, Scarasta, and Greaval being similar in most respects to those already described. A specimen from Bleaval-Mula ridge, however, shows well the occurrence of cores of pyroxene in the larger hornblende crystals. A specimen from the foot of the south slope of Mula is somewhat more basic. The rock contains little or no quartz, very abundant plagioclase (andesine or acid labradorite), hornblende in isolated crystals, and also forming an edging to a pale monoclinic pyroxene, along with which occurs also a strongly pleochroic hypersthene. Iron-ores occur more abundantly than usual.

In Voumasdale the ground is extensively peat-covered and exposures are poor, but along the new road on the south-east side of the valley good exposures can be examined. A specimen from the roadside just south of Druim na Caorach shows well the effects of granulitisation. It consists of quartz in granules, plagioclase, hornblende in sieve plates, biotite, and iron-ores.

On the same road, but nearer Loch na Moracha, this type of rock is seen to pass into one of similar type, but richer in garnet. The garnets may be as much as an inch in diameter and so numerous as to give a reddish tinge to the rock. The rock as seen in section appears to have been coarser in grain than the average, though now extensively granulitised. The quartz and felspar in part are represented by a granular mosaic, in which occur irregular flakes of green hornblende and probably also grains of pyroxene. The abundant garnet is often surrounded by a rim of peg-like hornblende in felspar. It often contains minute rod-like bodies in two sets at right angles to each other.



Rocks resembling the gabbro-diorite described occur also on the north-east side of the Toe Head ridge, and again on the south-west coast near the Sound of Stromay. A dyke-like mass of much the same character was noted at Borosdale Point in the Isle of Ensay. Similar rocks occur interbanded with other types on Mas Garbh, Bosival, and Sletteval.

It may be of interest to note that within the main area of gabbro-diorite north-west of Voumasdale two occurrences of other rocks were noted. On Meaval and on the pass to the north-west of that hill there is a lenticular area of rather fine-grained hornblende-gneiss with north-north-west foliation. Again on Bleaval on the summit and extending along the ridge to the south-east there is a broad band of fine-grained hornblende-gneiss or schist, which includes some fine-grained highly-garnetiferous bands reddish brown in colour. The hornblende-schist and its accompanying garnetiferous bands resemble in some respects certain of the rocks of the Loch Langavat valley.

South-east of Voumasdale, as already stated, other rocks make their appearance. These are frequently so garnetiferous that the garnets standing out in clusters on the weathered surface give a reddish tinge to the rocks and can be seen from a distance.

Thus on Beinn Tharsuinn, especially on the steep south face of the hill, very garnetiferous rocks are exposed. An example (Pl. IV, fig. 4) of these is seen to be made up, to the extent of two-thirds of its bulk, of garnet intergrown with green hornblende and pyroxene and granules of iron-ores. This rock, which may be described as an *eclogite*, is accompanied by others which may be called *garnet amphibolites*.

Dark hornblendic rocks generally garnetiferous are seen on the Bosival ridge. A typical example in hand-specimen is dark coloured with red blotches. It consists mainly of garnet, hornblende, and pyroxene, the latter occurring in small isolated crystals and also forming centres to the hornblende. The felspar, which is clear and fresh, appears to be mainly andesine and generally shows twinning, but occurs also in untwinned grains. The garnet is surrounded by and frequently crossed by bands of varying width, within which there is an intimate intergrowth on a small scale of hornblende and felspar. Within this intergrowth are strings of granules of iron-ores. These rocks resemble very much in character some of the bands of gneisses of igneous origin associated with the paragneisses of the south-western belt, as for instance the rock types running from Renish Point north-westwards to Obbe. They may represent the country-rock into which some of the other types described have been intruded.

The more acid bands which occur in association with the types just described may be illustrated by an example taken from near the margin of the anorthosite-gneiss about 200 yards north-west of Coire Roneval. The rock is of light colour, of medium grain, and unevenly granulitic, uneven grains or groups of grains of relatively large size forming half the rock, while the other half is granulitic on a fine scale. Quartz is the most abundant constituent. Plagioclase (oligoclase) is next in abundance. Garnet in irregular and much cracked grains occurs sparingly, while groups of small grains of hornblende and minute flakes of biotite occur still more sparingly. Small crystals of apatite and zircon occur as accessories.

#### (e) *Paragneisses and Associated Rocks of the Loch Langavat Valley.*

The well-marked valley occupied by Loch Langavat has been cut out of a series of gneisses and schists with a marked S.S.E.-N.N.W. strike and a dip sometimes vertical, but more usually steep to W.S.W.

These rocks are of interest because they frequently show banding so definite as to suggest that they represent a stratified sequence. They include, also, certain thin bands, such as

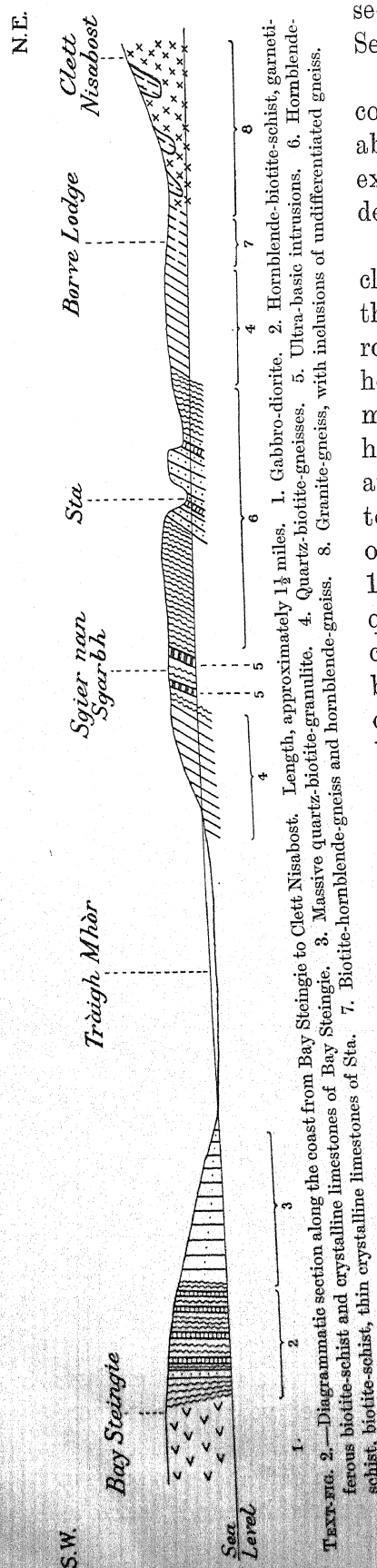
crystalline, limestones, biotite-schists, garnetiferous biotite-schists, which are probably of sedimentary origin, and resemble some of the rocks of the Rodil Series (Pl. V).

The best section of these rocks is seen on the north-west coast between Bay Steingie and Clett Nisabost. The section, about  $1\frac{1}{2}$  miles long, is incomplete, but, as it presents a better exposure of the rocks than can be found inland, it will be described first, beginning at the south-west end.

At Bay Steingie the rocks under consideration are seen close to the gabbro-diorite (already described), but as stated the nature of the junction has been obscured by shearing. The rock next to the gabbro-diorite is a glistening, fine-grained hornblende-schist traversed by narrow quartz veins. It is made up of granules of quartz, acid plagioclase, abundant hornblende, and contains in addition some granular sphene and apatite. Fine hornblende-schists of similar type dipping steeply to E.N.E., *i.e.* away from the junction, and having a breadth of outcrop of about 12 yards, follow, after which comes a band 12-14 feet thick, weathering brown. This is a fine-grained quartz-schist, reddish brown from the presence of garnet. It consists mainly of quartz, with some oligoclase felspar, garnet, biotite, and iron-ores. North-east of the garnetiferous band comes a breadth of about 5 yards of finely-banded hornblende-biotite-schist, followed by a crystalline limestone 8 feet thick. This limestone is grey in colour, well foliated, shows well-marked ribs on the weathered surface, contains occasional small white lumps of diopside, and encloses at least one narrow lenticle of red weathering biotite-schist (Pl. II, fig. 1). It is crossed near the seaward end of the exposure by a narrow vein of crumpled hornblende-biotite rock. The limestone is usually fine grained, but occasionally white and coarse. An average specimen consists of carbonates, mainly calcite, enclosing rounded grains and groups of grains of serpentinised forsterite. A few small flakes of a faintly pleochroic phlogopite occur, and also probably a little graphite.

The limestone is succeeded to the north-east by hornblende-schists like those which occur on the south-west side of it. They are fine grained and glistening on a fresh surface consisting of quartz, acid plagioclase, abundant hornblende, biotite, rather abundant granular sphene, with iron-ores and apatite.

The hornblende-biotite-schists north-east of the 8-foot limestone are in turn succeeded by a thin limestone, of which a thickness of about a foot is exposed. This is succeeded by fine hornblende-schists of the usual type, which extend to near a boundary wall on the south side of which are several thin bands of limestone, some white, accompanied by thin schistose bands. These bands contain a little quartz, plagioclase-felspar,



TEXT-FIG. 2.—Diagrammatic section along the coast from Bay Steingie to Clett Nisabost.

hornblende, reddish-brown biotite, iron-ores, and probably also a very small amount of graphite in the form of dust or in veinlets in the other minerals.

The beds described last are followed at the wall by a hard rib of rock light grey in colour, compact, and showing in hand-specimens occasional grains of pyrite. It consists of hornblende and monoclinic pyroxene in about equal proportions, these two constituents making up the bulk of the rock. In addition there is a blue polarising chloritic mineral, sphene in isolated granules and interstitial carbonates.

On the north-east side of this hard rib comes another group of thin impure limestone bands accompanied by fine-grained hornblende-biotite-schists. The most prominent of the limestone bands is a white, medium-grained rock with green spots. It consists mainly of calcite enclosing irregular masses of serpentinised forsterite. The accompanying schists, dark and fine grained, contain quartz in rounded grains, oligoclase-felspar, abundant hornblende, sparing brown biotite, apatite, and iron-ores. These thin limestones and their accompanying schists are crumpled and show wavy outcrops. North-east of them comes a massive brownish-grey well-foliated rock, which consists of dark micaceous streaks, alternating with thicker and more persistent laminæ white or sometimes pinkish in colour. Under the microscope the rock is seen to have a coarse granulitic structure. The dark laminæ consist of groups of flakes of brownish-green biotite, with which is usually associated rather abundant epidote and occasionally sphene. Occasional small crystals of a blue-green hornblende and small crystals of apatite also occur. The lighter parts of the rock consist of quartz and plagioclase (andesine). Iron-ores occur sparingly. This massive granulitic rock, cut by thin quartz veins, is interfoliated at its southern margin with narrow lenticles of hornblende-schist. A rock of similar type, not fully exposed and apparently more interbanded with hornblende-schist, extends across the bay to the Standing Stone. A rock which appears to be a continuation of the one last described is well exposed on the shore north-west of the Standing Stone. It is a massive granulitic rock consisting of quartz, plagioclase-felspar, hornblende, biotite, epidote, granular sphene, and a few granules of iron-ores. To the north-east this rock disappears beneath the sands of the Traigh Mhor and a wide gap in the section occurs. The dip of the beds, already described, at first steep to E.N.E. at the junction with the gabbro-diorite, soon becomes vertical and remains so as far as they are exposed.

North of the Traigh Mhor the next rocks met with are leaden-coloured quartzose-gneisses or schists, with occasional thin bands of hornblende-schist. These beds dip steeply to W.S.W. The grey quartzose-schists (Pl. II, fig. 3) consist of rather abundant quartz in irregular grains showing marked strain shadows, about an equal amount of felspar, which includes orthoclase, microcline, and acid plagioclase, a few flakes of greenish-brown biotite, with an equal amount of epidote. Granules of sphene and small crystals of apatite occur as accessories. The thin hornblendic bands which occur occasionally with those last described are fine grained and granulitic. Green hornblende is the most important constituent, epidote and biotite occur sparingly. Quartz is in the form of irregular strain-shadowed grains. Felspar includes orthoclase, microcline, and oligoclase. Granules of sphene and crystals of apatite also occur.

The rock types described above are well seen on the south side of Sgier nan Sgarbh, south of the outcrop of a large peridotite dyke, which forms a prominent feature on the shore at this point. North of the peridotite hornblende-schists of a type similar to those already described extend to Sta, on both sides of which red garnetiferous biotite-schists with hornblende-schists make their appearance. The rocks in the inlet of Sta are almost entirely concealed, but include in addition to a dyke a band of crystalline limestone, which, however, is only partly exposed. North of Sta another thin limestone occurs accompanied by thin biotite-



schists and hornblende-schists. North of these, but still south of the Borge Burn, come leaden-grey quartzose-schists, which resemble in hand-specimen and under the microscope the rocks which occur just north of the Traigh Mhor (Pl. IV, fig. 5). They contain, however, in addition, thin inconstant bands, which in the field resemble a reddish quartzite. These red bands do not differ greatly in composition from the grey rocks among which they occur. They contain quartz in irregular strain-shadowed grains, making up half the rock, cloudy feldspar (orthoclase and plagioclase), occasional clear grains of microcline, a few small flakes of green chloritised biotite, and a few granules of epidote.

From Borge Lodge to the north-east the chief rock is a grey coarse-grained hornblende-biotite-schist. A specimen cut by a group of pegmatites (Pl. II, fig. 4) from the shore south of the Borge Burn consists of quartz, orthoclase, and oligoclase, rather sparing biotite and hornblende, epidote, granular sphene, and apatite. To the north of the Borge Burn this, the main rock type along with hornblende-gneisses, has been invaded by a granite-gneiss, which from Clett Nisabost to Finsbay forms the north-east boundary of this group.

Inland to the south-east the beds just described are not so well exposed as on the coast, and the limestones in particular were not observed. The hornblende-schists, hornblende-biotite-schists, the grey quartzose-schists, and occasional bands of quartz-biotite-schist are exposed on the low pass to Loch Langavat south-east of Borge Lodge. They can be seen again near the north-north-west end of Loch Langavat and on the Sletteval ridge. Still farther south-east near the south-east end of Loch Langavat, and between the loch and Finsbay, brown quartzose-biotite-schists can occasionally be seen along with coarse and fine acid and hornblendic gneisses and schists. At this end, however, the outcrop is probably narrower than in the north-west, and the rocks appear to have been modified by the granite-gneiss. Bands and pillow-shaped masses of the granite-gneiss can be seen among them. They are cut by numerous pegmatites, and in addition shot through with veins and strings of acid material.

(f) *Ultra-basic Intrusions (Peridotites).*

Ultra-basic intrusions in dyke-like and sill-like forms and in lenticles were noted at several places. Usually they have been partly or wholly altered to serpentine and sometimes on their edges sheared into schists. The chief occurrences are noted on the map (Pl. V).

1. At Eilean Glas, Scalpay, a sill-like mass with a maximum thickness of 20 feet crosses the narrow isthmus between the two landing-places near the lighthouse. Like the gneisses amongst which it lies it has been somewhat sheared, especially at the edges, and contains here and there, particularly near the south-west end, irregular veins of steatite and small veins of fibrous chrysotile. A lenticular mass of similar character is seen on the coast south-west of the lighthouse.

2. Another example was noted on the mainland of South Harris near the north-east end of Loch na Uamha. This is a lenticle about 30 yards long, with a maximum breadth of 20 yards, weathering reddish brown with a rough carious surface, but compact fine grained and brownish green on a fresh face.

3. North-west of the last exposure and about 100 yards west of the footpath from Grose-bay to the main Tarbert road and near Loch Tollabreck, two prominent bands of reddish-brown serpentinous rock can be seen on the hillside. They appear to be two dyke-like masses trending north-west. The larger of the two is about 30 yards broad; the smaller about 10 feet. The outcrops at this locality are traceable for about 100 yards.

4. The largest and best exposure of this type of rock is that seen in the Loch Langavat

Valley, parallel to and just north-east of the loch. This mass, which appears to be a large dyke, can be traced from a few hundred yards south-east of the Scara Ruadh to the Dun near Borge Lodge, and from thence to the coast at Sgier nan Sgarbh. At the Scara Ruadh it is about 40 yards wide and forms a well-marked ridge, which, by reason of its reddish-brown colour, is prominent from a distance. Farther to the north-west it is narrower and probably branches, two bands being seen on the coast. Throughout its course it shows well the effects of pressure by movement, being pinched out at intervals and generally schistose on the edges. It shows also very fine glacial grooving and striae.

As all occurrences noted above appear to have been derived from similar rocks, a general description may be sufficient. In all of them specimens can generally be found, especially in the most massive parts and near the centre, showing that these rocks were originally made up mainly of olivine and rhombic and monoclinic pyroxene with iron-ores. They have also contained in most cases a micaceous mineral, now altered to chlorite, sometimes polarising in blue colours.

On their edges they have usually been converted into schists. A good example of this marginal modification is seen near the north-west end of Loch Langavat. Here the edge of the mass is a talcose schist with star-shaped groups of actinolite crystals lying along the plane of schistosity.

(g) *Granite-gneiss and Associated Rocks of Bulaval, Heilisval, An Coileach, Ben Luskentyre, and North-East Taransay.*

Over the greater part of the north-west portion of South Harris, and constituting about a third of the whole area described in this memoir, the ground is occupied to a predominant extent by granite-gneiss. This granite-gneiss is intrusive into acid biotite-gneisses and hornblende-gneisses which are seen forming a rim along the coast-line and appear also at several places inland (Pl. V). The granite-gneiss forms the greater part of all the high ground from Bulaval north-east to West Stocklett, the Luskentyre hills, and is well displayed in the north-east portion of Taransay. On the north-west and north sides it reaches the coast at several places. The boundary between it and the schists on the south-west appears to be nearly a straight line running through Taransay, and thence south-south-east from Clett Nisabost by Sletteval to near Finsbay. Along this south-west margin the acid-gneisses bordering the granite-gneiss and the granite-gneiss itself have been extensively granulitised, and the actual margin of the granite-gneiss is not easily determined.

One of these acid bands seen on the coast at Borge Lodge just north of where the stream enters the sea is a coarse acid-gneiss consisting of quartz, orthoclase, acid plagioclase, biotite and hornblende, rather abundant epidote, granular sphene, apatite, and iron-ores. The presence of hornblende distinguishes this band from the granite-gneiss proper.

Towards the south-south-east the boundary is more irregular. The south-east margin is highly irregular, for while on the high hills the granite-gneiss is massive and well defined, when followed to the south-east it becomes more and more involved with the gneisses of that area. Tongues and ribs of the granite-gneiss probably penetrate the gneisses of the eastern side to within a short distance of the east coast. On Ben Luskentyre, at the summit of Beinn Dhubh, the granite-gneiss weathers into huge tabular blocks owing to prominent joints, one set running from north-east to south-west, and the other from north-west to south-east.

The typical granite-gneiss is a light grey massive rock, with a streaky inconstant large-scale foliation visible in the field but not in hand-specimens. The strike of the foliation is south-east north-west.

Under the microscope (Pl. IV, fig. 6) traces of granulitisation are always seen. The rock consists of abundant quartz, generally in large ragged patches made up of groups of interlocking grains; feldspars including microcline, orthoclase, and a plagioclase (albite-oligoclase). The quartz and feldspars together make up the bulk of the rock. The next most abundant constituents are epidote in broken crystals and aggregated grains and irregular flakes of a greenish-brown biotite. Apatite, zircon, occasional grains of sphene, and rarely magnetite occur as accessories. Muscovite is present to a sparing extent in some sections and more plentiful in others. The rock throughout shows marked signs of pressure. The quartz displays wavy extinction, the twin lamellæ of the microcline and plagioclase are frequently bent and broken, part of the feldspars is sericitised and contains granules of epidote, and the flakes of mica are bent and torn.

The typical grey granite-gneiss from the top of Leathad Mor, 400 yards east of Uaval More, shows the same mineral assemblage but granulitisation of a more advanced stage. The mica and epidote have been drawn out into wisps and strings of granules, which wrap round distorted and strain-shadowed grains of quartz and feldspar.

The granite-gneiss just west of the sharp bend in the road south of Tarbert, known locally as the Devil's Elbow, is in a still more crushed condition, and here it is seen enclosing and veining a hornblende-gneiss.

Examples taken from different localities show that the granite-gneiss is everywhere very uniform in mineral composition.

On the island of Taransay granitoid gneiss and pegmatites are conspicuous in the larger and north-eastern portion of the island. It is well seen in a massive condition on the summit of Ben Raah, and on the slopes of that hill it occurs as broad bands and tongues intrusive into acid biotite-gneiss and dark hornblende-gneiss. The usual strike of the acid biotite-gneiss and dark hornblende-gneiss is north-west and south-east, but on Clett More the foliation is considerably disturbed by the granite-gneiss and by abundant pegmatites. The gneisses into which the granite-gneiss is intruded are also seen at places around the coast of this part of Taransay. These acid-biotite-gneisses and hornblende-gneisses are seen as a rim along the north-west coast-line of South Harris, from a little north of Borge Lodge to near Tarbert, but at places tongues of the granite-gneiss cut through them to the coast-line. Around the promontory of Ard Nisabost the foliation planes have the usual strike north-west to south-east, with a vertical dip. The granite-gneiss of the promontory with associated pegmatites is obviously intrusive into the gneisses seen around the rim.

On both sides of Traigh Luskentyre the gneisses forming the rim show the normal strike of the foliation planes with a dip to the south-west. These gneisses into which the granitoid mass is intruded appear inland in some of the hollows between the high hills, as for instance in the depression between Bulaval and Heilisval Beg. They crop out on Ben Luskentyre at various places on the lower slopes of Beinn Dhubh, and again between Ben Luskentyre and the head of West Loch Tarbert.

(h) *Gneisses of the South-east Coast of Harris and of the Isle of Scalpay.*

Along the south-east coast of Harris, north-east of Finsbay, and including the whole of Scalpay there is a belt of varying width where the granite-gneiss becomes interbanded with or replaced by other types of gneisses both basic and acid. Just along the coast-line, however, the rocks have been crushed to a varying degree, and there it is not always possible to distinguish between the granite-gneiss and other acid-gneisses. On the whole, in the



southern part of this belt the granite-gneiss with the associated pegmatites is most in evidence. Thus on Quidnish, north of Finsbay, on Ard Manish, Ard Mor, and Rudha Cluer, the granite-gneiss and pegmatites are prominent. Farther north-east, as around Seadabay and in the neighbourhood of Plocrapol, it is much less abundant, but even in Scalpay it probably occurs forming ribs among the other gneisses.

The other associated acid-gneisses are generally coarse in grain and are well displayed at many places along this belt, as, for example, at Kyles Stockinish, Loch Beacravik, and Geocrab, where a coarse foliated grey and pink biotite-gneiss is sometimes prominent.

Another type which is easily distinguished in the field from the others occurs most abundantly in the neighbourhood of Plocrapol, but is found also near the head of Loch Stockinish, on the coast east of Ardmeavaig south-east of Tarbert, and also on the south coast of Scalpay. In hand-specimens it is a coarse-grained, light-coloured rock with prominent crystals of black hornblende. Under the microscope the rock is seen to consist of abundant quartz drawn out and granulitised, felspar so crushed and cloudy from decomposition as to be indeterminable, hornblende dark green in colour and strongly pleochroic, epidote, occasional grains of sphene and some apatite.

Interbanded with the granite-gneiss and the other acid types mentioned are dark basic gneisses. These include coarse and fine hornblende-gneisses, hornblende-biotite-gneisses, hornblende-pyroxene-gneisses, sometimes granulitic, and in addition, but more rarely, schistose bands of a biotite-hornblende rock.

An example of the hornblende-gneiss interbanded with granite-gneiss on Rudha Cluer is dark and rather coarse grained and shows signs of crushing in hand-specimens. Under the microscope it is seen to consist of quartz drawn out and granulitised and showing marked strain-shadows; plagioclase-felspar crushed and cloudy from decomposition, abundant hornblende fresher than the other constituents, epidote in crystals and in veins, and in addition a little sphene.

The hornblende-biotite-gneisses may be illustrated by an example from the east side of Plocrapol Bay. This rock, which is partly crushed, consists of quartz, plagioclase-felspar, abundant greenish-brown hornblende, biotite subordinate to the hornblende in groups of small flakes, epidote in crystals, and also forming veins, iron-ores, and sphene.

Of the hornblende-pyroxene-gneisses showing granulitic structure good exposures can be seen on Ard Collam, Rudha Cluer. In hand-specimen it does not differ greatly in appearance from the medium-grained hornblende-gneisses, nor does it show in the field much evidence of crushing, though this is more obvious under the microscope. The rock has a typical granular structure, the granules, however, being of unequal size in different parts of the slide. It consists of quartz, andesine, abundant green hornblende, both monoclinic and rhombic pyroxene, the latter markedly pleochroic, garnet, and iron-ores.

Granulitic pyroxene-gneisses of somewhat similar type are seen also near Plocrapol and again in Scalpay.

Much rarer than the types mentioned are narrow bands of friable schistose rock. One of these from Rudha Bocaig may be described as a hornblende-biotite-schist.

#### (i) *Pegmatites.*

Throughout South Harris pegmatites are abundant and widely distributed. They form a prominent feature especially along the east coast, as on the promontories of Rudha Cluer and Quidnish, while inland their size and colour make them conspicuous objects on the hill-sides even from a distance.

Though found everywhere they have a marked concentration along certain lines. Their prevalence on Quidnish and other promontories on the east coast has been mentioned already. Along a narrow belt extending N.N.W. from near Finsbay by the Sletteval ridge N.E. of the Loch Langavat depression to the west coast they are specially large and numerous. What is probably a continuation of the same belt still farther to the N.N.W. is seen on the island of Taransay, where numerous pegmatites form a belt crossing the island just N.E. of the sandy isthmus between Loch na h-Uidhe and Traigh a Siar. It is to be noted that this N.N.W. belt of pegmatites in Harris with its probable continuation in Taransay lies just S.W. of the granite-gneiss. Along this belt the pegmatites in irregular dyke-like form stand vertically or nearly so.

Farther to the S.W. several large pegmatites form prominent features on the hills. Two of these are seen on Sletteval about a mile N. of Lingarabay. Several occur on the south-west slope of Beinn na h-Aire. Others are seen on the south-west coast opposite the island of Stromay. Another is seen on the steep face of Beinn Tharsuinn overlooking Loch na Moracha. Two large and several smaller ones form marked features on the south-east slope of Chaipaval. These large pegmatites, occurring sporadically S.W. of the main belt, frequently have a marked dip to N.W., which in conjunction with the form of the ground gives them a curving outcrop. They behave as sills cutting sharply across the foliation of the gneiss. This is well seen on Beinn Tharsuinn and again at the S.W. end of the pegmatites on Chaipaval. Many of these pegmatites as in the main belt and at Chaipaval are upwards of 20 feet in thickness.

The majority are light reddish or nearly white in colour, of coarse and uneven grain, crystals of felspar 4-6 inches in length being common. They are predominantly quartzofelspathic, dark minerals of any kind forming a small proportion of their bulk. Felspar is generally more abundant than quartz. They usually show a graphic intergrowth of quartz and felspar, and nearly all show more or less signs of crushing.

As these large pegmatites are all very much alike they may be described together. The felspar is usually microcline, sometimes orthoclase, enclosing in perthitic fashion a plagioclase near albite. The perthitic structure is often visible in hand-specimen, but also occurs on a microscopic scale. The only other common constituent is a dark mica in rather small and irregular plates, and another constituent, though less common than the mica, is magnetite in irregular masses an inch or more in length. Where, as along the east coast, the pegmatites have been subjected to more than the usual amount of crushing, granules and sporadic crystals of epidote may be developed.

An example of rather different type is seen on the S.W. face of Beinn na h-Aire immediately S.W. of the anorthosite-gneiss mass. It shows marked signs of crushing, the quartz drawn out and granulitised with wavy extinction. The felspar, mainly oligoclase, is much strained and contains numerous minute rod-like inclusions. Where the felspar has been crushed it is cloudy from the presence of granules of epidote. There also occur sparingly crystals of a dark mineral, probably originally hornblende now chloritised, with which are associated granules and crystals of epidote.

Certain small pegmatites were noted especially on the S.W. coast. These are marked by their smaller size and finer grain, but especially by the light blue or opalescent colour of their felspars. One of these seen on the steep slope N.E. of Stuaidh near Rodel consists of orthoclase and microcline enclosing blebs of quartz or in graphic intergrowth with it, also sparing oligoclase and granular epidote. The pegmatite has undergone considerable crushing and granulitisation.

At several localities, as on the south side of the isthmus at Tarbert and again on the roadside  $\frac{1}{4}$  mile W. of Loch na Creige Glaise, a reddish, coarse acid-gneiss occurs which appears to be pegmatitic in character. An example from the last-named locality consists of sheared and granulitised quartz, crushed orthoclase, and acid plagioclase, with abundant granular epidote.

(j) *Zones of Crushing.*

In previous memoirs on the southern parts of the Outer Hebrides a description was given of a marked zone of shearing along the eastern parts of the islands. Within this zone the rocks show all stages of crushing, including the formation of mylonites and flinty crush-rock. Occasionally where the crushing has been accompanied by fusion, pseudo-tachylyte has been formed. In South Uist and in North Uist the crushed zone has a well-marked base which has been mapped as a thrust-plane. This great zone of crushing, last seen at the north-east end of North Uist at Crogary na Hoe, was traced as far as the small islands on the south side of the Sound of Harris and was found to include Hermetray and part of the island of Vaccasay. There is evidence that this belt of crushed rock continues north-east into the area dealt with in the present paper (Pl. V). Here, however, the crushed zone has no clearly marked base, and the crushing is not usually so marked as farther south.

Extensive crushing was noticed on the island of Gilsay. This small island lying near the centre of the east end of the Sound of Harris shows on the west side vertically-banded acid and hornblendic gneisses, with the usual north-west or north-north-west strike. The south-east part of the island, on the other hand, has the gneisses much twisted and disturbed, while a ridge a short distance from the east side is made up of gneisses and pegmatites crushed and sometimes reduced to green mylonites. The neighbouring skerry, Dun-aarin, shows much disturbance of the gneiss and probably lies within the same zone of disturbance.

Farther north on Renish Point the rocks are crushed and shot with small veins of flinty crush material or pseudo-tachylyte. The paragneisses and associated rocks on the south-east side of the Isle of Vallay are crushed and mashed together.

On Rudha Vallarip the effects of crushing are well seen, the rocks on the seaward face of the promontory being reduced to a platy green mylonite, with strike to the north-east and dip to the south-east. The crushing, however, is not confined to the coast, but extends inland to west of the Rodil-Finsbay road. The anorthosite-gneiss loses its characteristic rough-jointed weathered surface, and with the quartzose pegmatites which occasionally cut it becomes a splintery white porcellanous rock. A marked zone of shearing with development of much flinty crush-rock is seen west of the road along the steep N.-S. face east of Stuigha. Just west of Loch Vallarip the crushed anorthosite-gneiss and associated rocks form a pseudo-breccia veined in the usual manner by flinty crush material. Crushing of similar type can be seen around Lingarabay.

North of Lingarabay, as at Cnoc Mor Hal and Sron Ghaoithe, the rocks have been crushed, and occasionally in consequence have a north-east foliation superinduced upon them. This is best seen on the coast at Cnoc Mor Hal. To the west of this superinduced foliation is a belt where the rocks appear massive and without definite foliation in the field, though evidence of crushing is seen under the microscope. To the west of this zone the normal N.N.W. foliation is undisturbed.

Farther north-east, on the promontories such as Quidnish, Ard Manish, Ard Mor, and Rudha Cluer, the crushing is not obvious in the field, but is usually shown in microscopic sections.



Around Scadabay and Plocrapol the area affected by crushing is much wider than farther south, but the degree of crushing varies considerably. On Plocrapol Point a north-east foliation has sometimes been superinduced on rocks that have undergone crushing, but farther south, as at Camas na Roide and on Rudha Bocaig, considerable areas occur where the foliation has the usual N.W.-S.E. strike, though even here narrow belts of crushed rock lie between relatively uncrushed portions. The gneiss in this district is highly jointed, the main joints running N.-S., while the smaller joints tend to be irregular but trend mainly E.-W. The surface is very broken with numerous hillocks showing steep faces—a type of scenery like that displayed in the Isle of Ronay off North Uist. This is well exemplified on the south-east coast of Harris at the head of Loch na Uamha.

On the promontory between Loch Scadabay and Loch Grosebay the gneisses show varying stages of crushing, a marked belt running north from the north-west end of Scadabay. Along the north-east side of Loch Grosebay crushed bands alternate with others less affected. On the steep face of the promontory there is much evidence of shearing and of numerous small reversed faults accompanied by well-developed jointing.

It is worthy of note that many of the rocks of this belt, which appear massive and undeformed in the field, when examined under the microscope show obvious signs of shearing. The quartz is drawn out and granulitised, the feldspars crushed and decomposed, but the dark minerals are less affected.

On the Island of Scalpay evidence of shearing by movement from the south-east is abundant and clear. At Eilean Glas near the lighthouse the prevalent acid and hornblende gneisses have been sheared into platy rocks, but not usually reduced to mylonites. The strike of the new foliation is north-east, with steep dip to the south-east. Farther north on Greinen, north of Scoravick and on Ard Riabhach, the grey acid-gneiss, hornblende-gneiss, and pyroxene-hornblende-gneiss, the pegmatites and occasional quartz veins have been sheared and have developed a north-east strike and dip to the south-east. Just west of this belt is a narrow zone where the gneisses are markedly jointed. West of the highly-jointed zone the usual north-west foliation is resumed.

It appears, therefore, that the south-east coast of South Harris and the eastern part of the Isle of Scalpay are on or near the great zone of shearing, which is better displayed in the isles farther south. The movements which produce the crushing appear to have been from south-east to north-west.

In addition to this crushed zone bordering the south-east coast several narrow crush bands were observed in South Harris which have a general north-west trend. The positions of the more important of these are marked on the map. Though of little breadth they have had an important effect on the topography, for, as a result of erosion, they lie now in well-marked valleys cut occasionally to near sea-level. Along these bands the rocks may be brecciated, drawn out, or occasionally reduced to mylonites, but flinty crush-rock appears to be rare.

On Scalpay, at Scoravick, a belt of splintery green mylonite about 20 yards wide is exposed on the shore, and strikes W.N.W. through the hollow marked by a chain of lochs. On the same line of strike a crush band crosses the narrow isthmus at Tarbert, being well seen on the south side of the valley at the heads of East and West Loch Tarbert. Another narrow one was noted running from Loch Ceann Dibig towards Bagh Stioclett.

A well-marked crush zone occupies the hollow along which the main road passes from the south-east to the north-west coast. It is occupied by Loch Bearasta Mor and other smaller lochs, and farther north-west forms the Laxdale valley. The crushed material can be seen on both sides of the road near the loch named, and still better near the head of Laxdale.

Another forms the Bealach Teoravait, and smaller examples can be seen in the higher passes to the south-west, *e.g.* Bealach Garbh.

Evidence of crushing by movement, however, is not confined to the examples mentioned, but occurs in varying degree throughout the area described. Thus considerable shearing can be seen along the south-west face of Roneval, on the Toe Head, and at the junction of the gabbro-diorite, with hornblende-schists at Bay Steingie. The granite-gneiss itself generally shows throughout its outcrop traces of crushing and granulitisation by movement.

## 2. MINOR INTRUSIONS OF LATER AGE.

Minor intrusions, generally in the form of dykes, which are later than the movements affecting the gneiss, are fairly numerous and evenly distributed throughout the area.

The general line of strike is S.E.-N.W. or S.S.E.-N.N.W. A few strike nearly N. and S., or even N.E.-S.W., but this difference in trend does not, so far as observed, involve difference in character.

They vary in thickness from less than a foot up to 30 feet. The average thickness of 50 measured was 10 feet.

Some of the larger dykes, though not very prominent on the coast, yet form prominent features inland, especially on the bare rocky ground of the Braigh nam Bagh and farther N. One example, seen on both sides of the road N. of the head of Loch Stockenish, is especially prominent, and numerous examples of the same kind can be seen along the ridge from Bulaval N.E. to West Stocklett.

Our collections include the following types:—

*Olivine Dolerites*.—These are by far the most common. They are generally markedly ophitic or, as in the case of the large dykes, have large feldspars or groups of feldspars well zoned and containing brown inclusions, probably glass, in a matrix of somewhat finer grain which shows ophitic structure. The amount of olivine present varies somewhat, and some show a small proportion of finely crystalline but generally decomposed groundmass.

*Olivine Dolerites (Crinan Type)*.—These are fairly common, more especially on the Island of Scalpay. They show the usual ophitic structures—the purple or plum-coloured pyroxene, labradorite-feldspar, with more acid margins, abundant olivine altering to yellow-brown serpentine, apatite, iron-ores, and a variable proportion of analcime.

Examples of this kind are: The 4-foot dyke running nearly N. and S. on Greinen Scalpay, the small dyke beside the lighthouse on Glas Eilean Scalpay, and the 10-foot dyke S. of Ben Scoravick on the south coast of Scalpay.

*Tholeiites*.—A few dykes are marked by the absence of olivine. In these a pale granular augite and plagioclase-feldspar make up the bulk of the rock. They are noteworthy in that they contain a noticeable amount of brown glass occurring interstitially and also in vesicles. In the vesicles this glass is accompanied by a dark green amorphous material, which resembles the chlorophæite of Dalmahoy and Kaimes,\* near Edinburgh.

Examples of this type are the 10-foot dyke on Eilean Quidnish and the somewhat larger dyke on the west side of Aird Harnasaig, Loch Grosebay.

*Lamprophyres*.—A few small rather decomposed dykes should probably be included here. The freshest of these is a small dyke from near the summit of Roneval. It consists of large crystals or groups of crystals, sometimes forming a cross, of a pale brown augite in a groundmass of much decomposed plagioclase. Small crystals of a reddish-brown hornblende and

\* CAMPBELL and LUNN, *Min. Mag.*, vol. xx, No. 110, p. 435.

still smaller flakes of biotite occur sparingly. Grains of epidote, magnetite, and pyrite, and numerous fine needles of apatite are noticeable. The rock throughout is cloudy from abundance of secondary carbonates. Vesicles are filled with calcite and quartz, and grains of quartz occur sporadically through the rock. The rock may be described as an *Augite Lamprophyre*.

#### IV. GLACIATION.

The glacial phenomena of South Harris are very similar to those already described in the islands forming the southern part of the Outer Hebrides. The upper part of the *mer de glace* moving out from Skye and the mainland across the Minch passed over South Harris in a direction from south-east to north-west. It buried the whole region except the tops of the highest mountains, which must have stood like nunataks above the general surface of the ice. For the most part the rock surfaces are bare of drift and present mamillated and smooth surfaces or *roches moutonnées* on the south-west slopes of the hills, while the north-eastern slopes are more irregular and less glaciated. These features are particularly well displayed along the south-east coast and again on the hilly ground bordering the west coast.\* Striae are numerous and usually trend from S.E. to N.W., but a few run more or less N. and S., the latter occurring usually on vertical joint faces. A number of these striae are indicated on the map (Pl. V). Deposits of drift occur at many places, chiefly on the lee or north-western side of the hills, but pockets of irregular patches are also found in the region bordering the south-east coast. Some of the principal localities in which considerable deposits of drift occur may be mentioned. A cliff of drift 20 feet high was found at the north-west end of the Isle of Killegray, and a cliff 10 feet high was again noted near the west of the Manish Strand at the north-west extremity of the Isle of Ensay. A low bank of boulder clay occurs on the north-east coast of this island at Bagh a Cotan, and the sea is cutting into another low bank of boulder clay on the east coast of the island south of Otternish. Good stiff boulder clay with included stones of local origin was exposed in excavations connected with road-making and the harbour of Leverburgh, and this extends up the valley to Loch na Moracha, being well seen on the slopes east of the loch and underlying the peat on the loch side. Cliffs of boulder clay 20 feet high, with some angular blocks of local rock, overlook the shore at Traigh na h-Uidhe south-east of Chaipaval; a few of the included boulders were striated. Quartzite pebbles are fairly common on the beach below, evidently derived from the cliff, for some examples were still found embedded in the drift. On the beach of this locality there lie a few large boulders of granite and some boulders of the anorthosite rock. Much of the low ground separating the Toe Head promontory from the main body of South Harris consists of drift material and blown sand. The slopes between this locality and Scarastavore are covered by skin and drift. As exposed on the roadside, the drift attains at places a depth of 10 feet. It is a fairly typical boulder clay with some angular boulders of local rock. The boulder clay passes under the sand dunes bordering the shore. In this neighbourhood some old gravel pits were noted in the drift.

Farther north on the west coast a cliff of drift 15 feet high was noted on the south-west side of Ard Nisabost promontory and a cap of drift with blown sand covers the whole of the promontory. A thin skin of drift lies on the slopes of the hills between Ard Nisabost and Traigh Luskentyre; there is a considerable exposure of rubbly drift on the south side of West Tarbert Bay at its head near the pier. Some rubbly drift is exposed in the bay to the east

\* Some of the most beautifully glaciated and striated surfaces in South Harris are seen on the band of peridotite rock just north of the north-western extremity of Loch Langavat.



of Diraclett on East Loch Tarbert. In the Isle of Scalpay blue-grey rubbly drift occurs at several places on the north coast, and on the west coast in the little bay north of Ard na Cille peat is seen resting on a sticky stoneless clay traversed by rootlets.

The only boulders foreign to the district that were noted were quartzite pebbles and boulders of red sandstone (possibly Torridonian), found very rarely along the western side of South Harris. The only evidences of local glaciation observed were some moraines lying to the east of Traigh Luskentyre and again north of Roneval, where a local glacier may have existed in Coire Roneval, for here there is evidence of the travel of boulders of local rock for a short distance in a northerly direction.

As already mentioned, the numerous small lochs which are scattered profusely in the comparatively low-lying tract bordering the Minch are of glacial origin, the great majority of them being rock basins trending on the whole in the direction of the main ice movement. A few have their waters held up in part or entirely by deposits of drift and peat. Loch Langavat, the largest loch in the area, is obviously a rock basin, having the form of a long, narrow trench trending from S.E. to N.W. The Obbe and the lochs to the north appear also to be partly at any rate rock basins.

#### V. ACKNOWLEDGMENTS.

We are indebted to the Northern Lighthouse Commissioners for permission to stay at the lighthouse on Scalpay Island.

During our sojourn in South Harris we received much assistance from Mr DAVID JONES, C.B.E., of the Fishery Board for Scotland, and from Mr ROBERTSON, factor, Tarbert.

Mr STEWART of Ensay very kindly gave us facilities for visiting the isles in the Sound of Harris, and Mr VENABLES of Luskentyre Lodge, and the Rev. Mr KERR of Scarastavore Manse rendered us valuable help.

Acknowledgment is due to the Carnegie Trust for a grant to defray expenses incurred in the preparation and reproduction of the illustrations.

#### VI. EXPLANATION OF PLATES.

##### PLATE I.

Fig. 1. Crystalline limestone near St Clement's Church, Rodil, showing rough surface and enclosed nodules of diopside.

Fig. 2. Anorthosite-gneiss; south side of Coire Roneval, showing rough weathering and streaky foliation.

Fig. 3. Anorthosite-gneiss; Coire Roneval, showing dark bands and lenticles.

Fig. 4. Gabbro-diorite; Rudha Liath, north-west coast. The photograph shows massive jointing, garnets, and irregular veins of hornblende.

##### PLATE II.

Fig. 1. Crystalline limestone; Bay Steingie, north-west coast, showing banding and weathering. On the right are fine-grained hornblende-schists.

Fig. 2. View to the north-east from Rudha Liath. The gabbro-diorite is in the foreground, the bay and low shore of the middle distance marks the position of the paragneisses and associated rocks of the Loch Langavat valley. In the distance are seen Clett Nisabost and the Luskentyre Hills, composed mainly of granite-gneiss.

Fig. 3. South side of Sgier nan Sgarbh, looking north-west. Shows quartz-biotite-schists or gneisses dipping steeply to the south-west.

Fig. 4. View of the beach at Borve Lodge, looking south-east. The photograph shows quartz-biotite-schists and hornblende-biotite-schists dipping to the south-west and cut by a pegmatite.

## PLATE III.

Fig. 1. Crystalline limestone; quarry, St Clement's Church, Rodil. The rock consists of forsterite partly serpentinitised, pyroxene, phlogopite, and pyrite in a groundmass of coarse and fine carbonates. Ordinary light.  $\times 20$  diameters.

Fig. 2. Fine-grained ferruginous quartz-schist; quarry, St Clement's Church, Rodil. The slide shows quartz in irregular grains, fresh and decomposed felspar, abundant biotite, garnet, flakes of graphite, and grains of pyrite. Crossed nicols.  $\times 27$  diameters.

Fig. 3. Quartz-felspar-biotite rock north of the piers, Rodil. The slide shows abundant quartz, felspar including microcline, biotite, and disseminated pyrite. Crossed nicols.  $\times 27$  diameters.

Fig. 4. Quartz-garnet-sillimanite rock; the Obbe, Leverburgh (fine-grained part). Shows abundant quartz, felspar, biotite, and fibrous sillimanite. Crossed nicols.  $\times 48$  diameters.

Fig. 5. Quartz-garnet-kyanite rock; Chaipaval. Shows abundant quartz, garnet, kyanite, biotite, and microcline. Crossed nicols.  $\times 27$  diameters.

Fig. 6. Hornblende-pyroxene-garnet rock; St Clement's Church, Rodil. The slide shows plagioclase, hornblende, pyroxene, and garnet. Ordinary light.  $\times 20$  diameters.

## PLATE IV.

Fig. 1. Anorthosite-gneiss; Roneval. Light part of rock. The slide shows labradorite-felspar. Crossed nicols.  $\times 27$  diameters.

Fig. 2. Anorthosite-gneiss; Beinn na h-Aire—dark part. The slide shows pyroxene, hornblende, and garnet, the latter fringed by an intergrowth of hornblende and felspar. Ordinary light.  $\times 20$  diameters.

Fig. 3. Gabbro-diorite; south side of Bay Steingie. The slide contains quartz, plagioclase, hornblende sometimes with a core of pyroxene, biotite, iron-ores, and apatite. Ordinary light.  $\times 20$  diameters.

Fig. 4. Eclogite; Beinn Tharsuinn. The slide shows garnet, hornblende, pyroxene, and iron-ores. Ordinary light.  $\times 20$  diameters.

Fig. 5. Quartz-biotite-schist; shore, near Borge Lodge. The slide shows quartz, felspar (orthoclase and plagioclase), biotite, sphene, and pyrite. Ordinary light.  $\times 20$  diameters.

Fig. 6. Granite-gneiss; roadside three-quarters of a mile north of Borge Lodge. The slide shows abundant quartz granulitised, orthoclase, microcline and oligoclase, biotite, muscovite, and epidote. Crossed nicols.  $\times 27$  diameters.

## PLATE V.

Geological Map of South Harris.

Professor T. J. JEHU and Mr R. M. CRAIG on "Geology of the Outer Hebrides."—PLATE I.

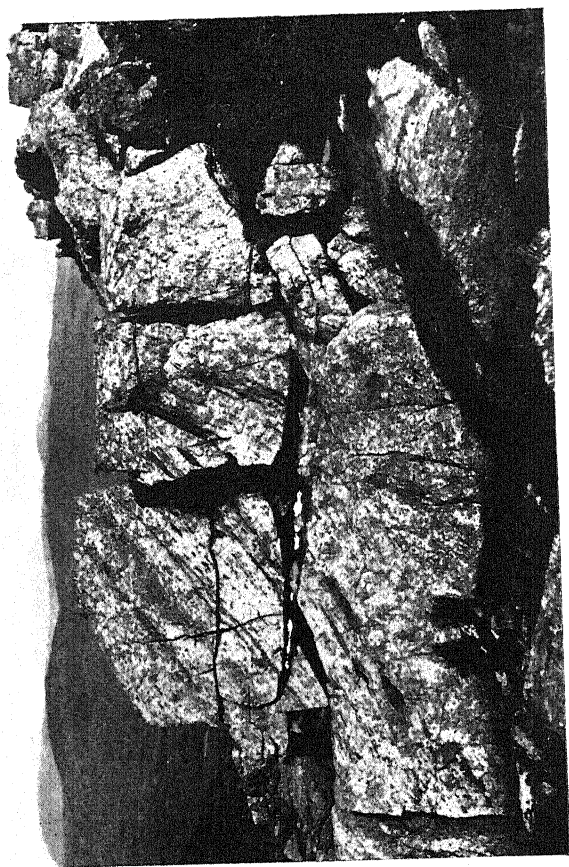


FIG. 2.



FIG. 4.



FIG. 1.



FIG. 3.





Professor T. J. JEHU and Mr R. M. CRAIG on "Geology of the Outer Hebrides."—PLATE II.



FIG. 2.

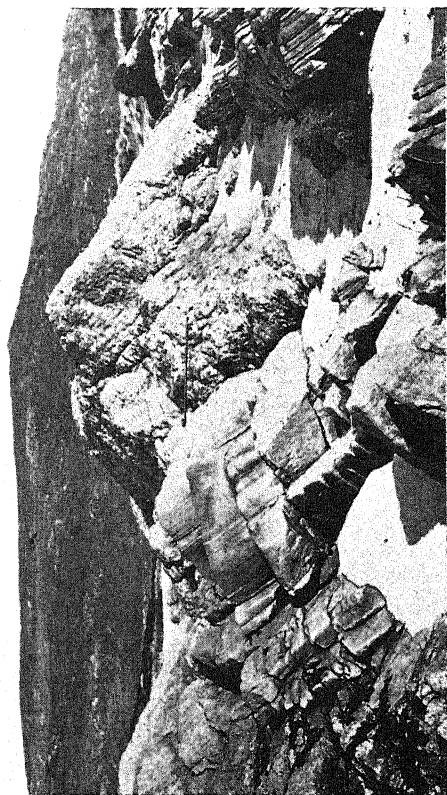


FIG. 4.



FIG. 1.



FIG. 3.





Professor T. J. JEHU and Mr R. M. CRAIG on "Geology of the Outer Hebrides."—PLATE III.

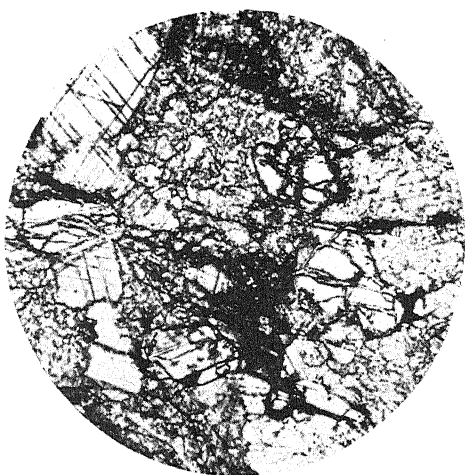


FIG. 1.

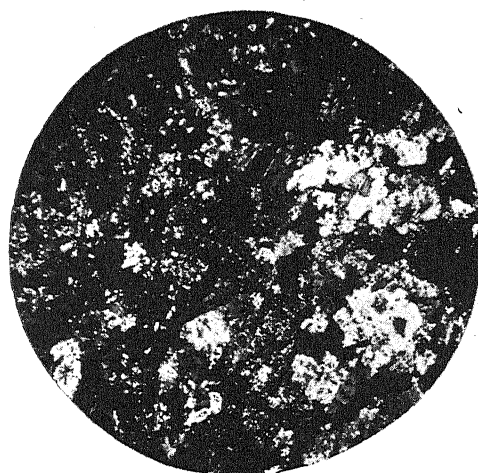


FIG. 2.

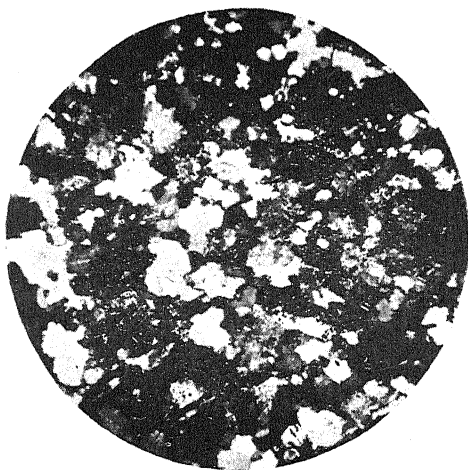


FIG. 3.

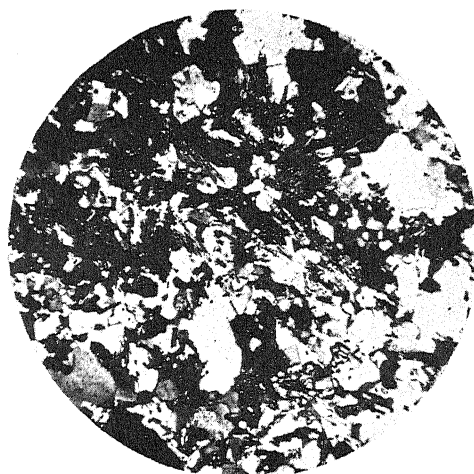


FIG. 4.

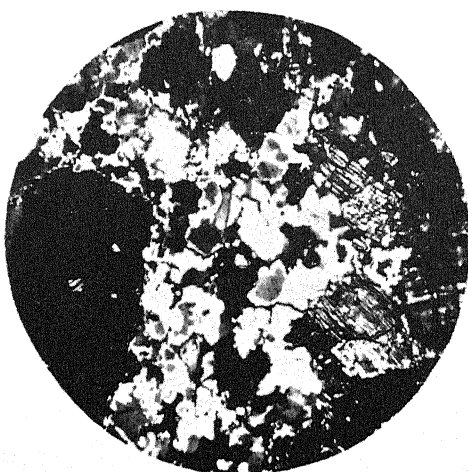


FIG. 5.



FIG. 6.



Professor T. J. JEHU and Mr R. M. CRAIG on "Geology of the Outer Hebrides."—PLATE IV.

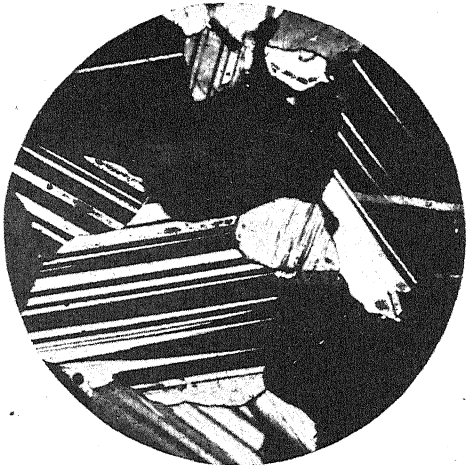


FIG. 1.

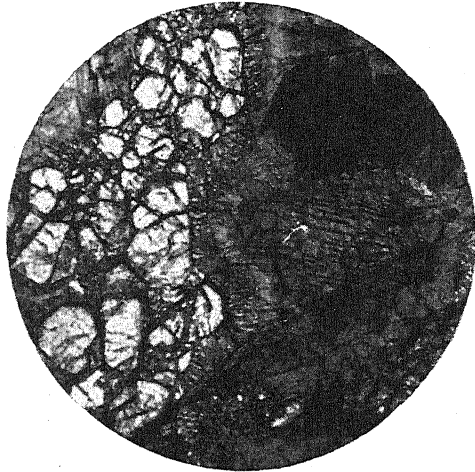


FIG. 2.

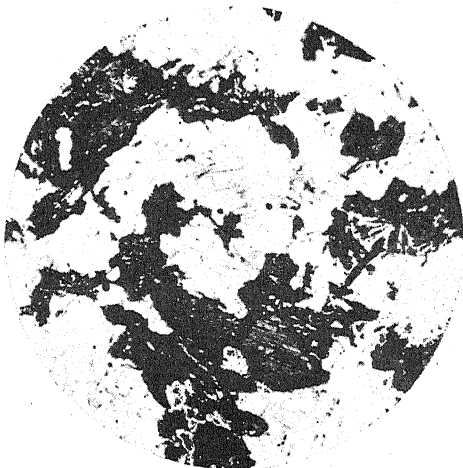


FIG. 3.

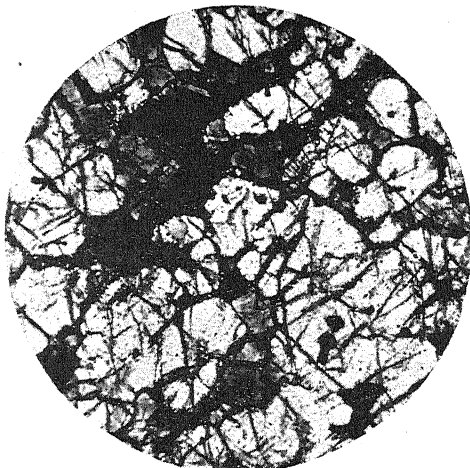


FIG. 4.

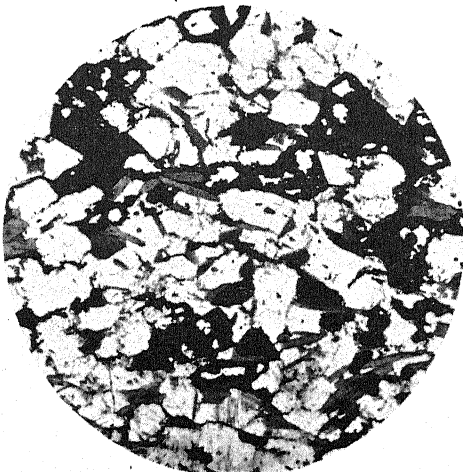
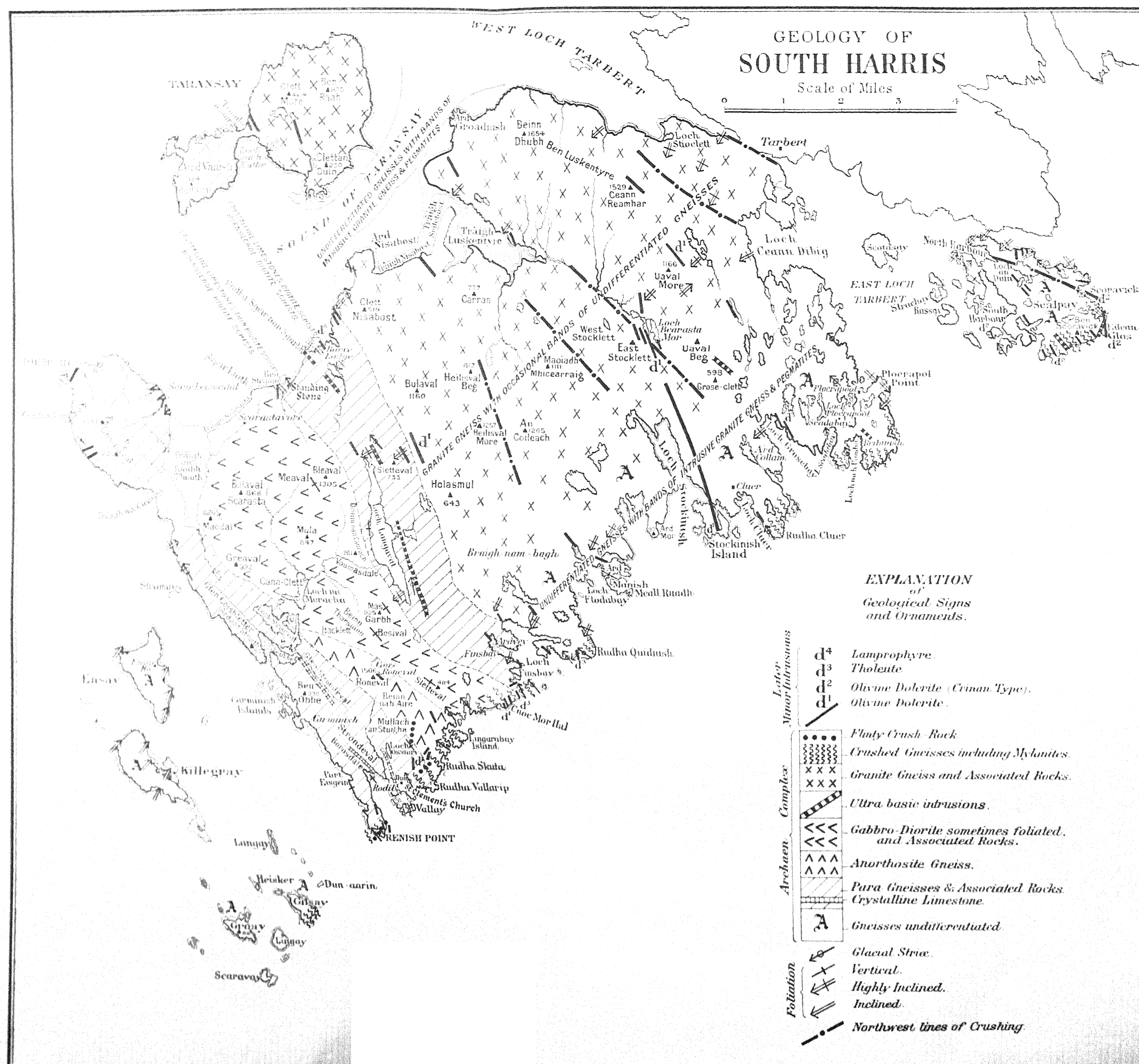


FIG. 5.



FIG. 6.







XXI.—The Tholeiites and Dolerites of the Dalmahoy Syncline. By Robert Campbell, M.A., D.Sc., and James W. Lunn, B.Sc., Ph.D. (With Two Plates and One Text-figure.)

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## I. INTRODUCTION.

The shallow synclinal fold termed the Dalmahoy syncline is situated between the north-western flank of the Pentland Hills and the Murieston fault, the most southerly of the five important easterly and north-easterly dislocations which traverse the oil-shale field of West Lothian. The core of the syncline is occupied by rocks belonging to the lower division of the Oil-Shale Group of the Lower Carboniferous. Intervening between these and the Cementstone Group is a volcanic zone, probably on the same horizon as the Arthur's Seat lavas, consisting mainly of mugearites and basalts which show their greatest development in the Corston Hill district. Along the whole of the southern limb of the syncline is an extensive spread of Upper Old Red Sandstone, but this formation is almost entirely cut out in the northern limb by the Murieston fault, appearing only in the core of a small anticline near Selms.

Associated with the bedded rocks of the syncline are several intrusive sills which belong petrographically to a single suite quite distinct from the quartz-dolerites and teschenites of the Edinburgh district, and which form the subject of the present communication. The largest intrusion extends through the conspicuous hills of Ravelrig, Dalmahoy, and Kaimes. Others occur at Kirknewton, Selms, Auchinoon, and Camilty (see map, text-fig. 1).

## II. PREVIOUS INVESTIGATION.

In his *Essai Géologique sur L'Écosse*, A. BOUÉ gave a description of the rocks of Dalmahoy which he regarded as varieties of phonolite (*Klingstein*). He recorded the occurrence of "a green mineral\* which possesses the singular property of passing very quickly on exposure to air to brownish black, then to black, taking on here and there in this passage a metallic lustre quite like that of *diallage metalloïde*," and quoted the opinion of M. CORDIER regarding the cause of the colour change. The observation is of interest since the mineral, which we now regard as identical with the chlorophæite of MACCULLOCH,† is one of the chief constituents of the Dalmahoy tholeiites but has been overlooked in all the modern descriptions of the rocks.

CHARLES MACLAREN described the "trap rocks" of Auchinoon and Dalmahoy in his *Geology of Fife and the Lothians*. He seems to have been puzzled by the unusual characters of the Auchinoon rock,‡ and found it "interesting as exemplifying the process by which some varieties of the trap family have been produced." "It seems probable," he said, "that in the Auchinoon rock we have nature caught in the fact, as it were, or the process of converting slate clay into greenstone arrested when half completed." It is clear from the details

\* *Essai Géologique sur L'Écosse* (circa 1820), pp. 127 and 157.

† *A Description of the Western Isles of Scotland*, 1819, vol. i, p. 504.

‡ *Geology of Fife and the Lothians*, 1st ed., 1839, pp. 171-173; and 2nd ed., 1866, pp. 234-236.



of his description that MacLAREN's relict pieces of "slate clay" are nodules of chlorophæite and chlorite.

The earliest account of the microscopic characters of the rocks is given by ALLPORT.\* He sectioned the rocks of Dalmahoy Hill and Kaimes Hill, and described them as consisting of plagioclase, augite, magnetite, and yellowish-green pseudomorphs of olivine, with apatite occurring sparingly. He found also that "the spaces between the larger constituents are filled with a felsitic and cryptocrystalline mass instead of the usual glass; in one section this substance also occurs as a small vein and is crowded with minute hexagonal plates of specular iron."

Sir ARCHIBALD GEIKIE † published a coloured figure of a slice of the Dalmahoy rock as representing some of the more salient characters of the local dolerites, and, in the accompanying explanation, referred to the considerable proportion of groundmass interposed between the various minerals. He recognised also that the crystals of iron oxide were titaniferous. A brief account of this rock, based mainly on ALLPORT's description, is given by Sir J. J. H. TEALL.‡

A more detailed description of the microscopic characters of the rocks of the Dalmahoy intrusion has been given by Sir JOHN S. FLETT,§ who observed that the serpentinous pseudomorphs after olivine sometimes contain undecomposed fragments of that mineral. Although he included it in his group of olivine-dolerites, FLETT stated that in its petrographical characters the Dalmahoy sill was not very closely related to any other rock of that group in the Edinburgh district.

T. CUTHBERT DAY discovered the presence of selvages of tachylite || at the base of the Dalmahoy sill at Ravelrig Quarry and along the margins of an offshoot from the main sill at Kaimes, and he has published also an account of the Auchinoon sill.¶ The occurrence of chlorophæite in the rocks of Dalmahoy and Kaimes Hills has been recorded by the authors \*\* in a paper in which they discuss the physical and chemical properties of that mineral.

### III. FIELD CHARACTERS.

*Dalmahoy Intrusion.*—The largest of the sills is the one situated about half a mile west of Balerno and usually spoken of as the Dalmahoy intrusion. Extending along the strike for fully 2 miles, it has a thickness of over 150 feet and embraces the conspicuous hills of Ravelrig, Dalmahoy, and Kaimes. The last two hills attain a height of over 800 feet. The tholeiites have been quarried for setts, curbs, and road "metal" for many years. At present two large quarries, Ravelrig and Kaimes, are being worked, and there are several disused quarries, two of them of considerable size, namely Hannahfield Quarry at the east end and Sheds's Quarry near the west end of Ravelrig Hill. Topographically the most outstanding feature is the bold columnar escarpment along the northern face of Dalmahoy Hill, which is repeated, although in less striking form, in Kaimes Hill to the west. The hollow between these two hills marks the course of a dip fault, and an oblique fault has determined the abrupt termination of successive escarpments at the western limit of Ravelrig Hill. On the southern aspect of the hills the bare dip slopes are intensely ice-moulded and show many glacial grooves which trend a little north of east.

Textural, and in lesser degree mineralogical, variations in different parts of the sill are

\* *Quart. Journ. Geol. Soc.*, 1874, vol. xxx, p. 555.

† *Trans. Roy. Soc. Edin.*, 1879, vol. xxix, p. 517.

‡ *British Petrography*, 1888, p. 190.

§ "The Neighbourhood of Edinburgh," *Mem. Geol. Surv. Scotland*, 1910, p. 291.

|| *Trans. Edin. Geol. Soc.*, 1920, vol. xi, pp. 16-17.

¶ *Ibid.*, 1920, vol. xi, pp. 51-53 and 128-130.

\*\* *Min. Mag.*, 1925, vol. xx, pp. 435-440.

very marked, and it is possible to distinguish in the field types ranging from tachylyte through basalt to tholeiite of varying coarseness, dolerite, and dolerite-pegmatite. There is considerable diversity also in the character of the jointing. One zone is characterised by the perfection of its columnar jointing, in places the rocks have a well-marked platy jointing, elsewhere the dominating joints are vertical but widely spaced. The variations in textural and structural characters are reflected in the minor topographical features, which suggest strongly that the sill is made up of a succession of intrusions. In Kaimes Hill, for example, where the dip is low and where only the lower half of the sill has escaped denudation, the following upward succession is seen in the eastern portion of the hill: (a) Coarse tholeiite passing gradually towards the base into "white trap"; (b) basalt; (c) medium-grained tholeiite, with occasional schlieren of coarse tholeiite, traversed by an extraordinary abundance of segregation veins and showing good columnar jointing; (d) dolerite. Zones (b), (c), and (d) outcrop on both the northern and southern aspects of the hill. On the southern working face of Kaimes Quarry the jointing in (c) becomes horizontal. The horizontally jointed rock can be followed for some distance around the southern base of the hill when it forms a distinct minor feature, suggesting that sheet (c) is here assuming a dyke-like character with a transgressive relation to (a) and (b). The basalt zone is well exposed in a small disused quarry opposite the termination of the track which leads to the hill from the Lanark road.

In Dalmahoy Hill the dip of the sill is much steeper, and higher zones are preserved.

Zones (a) and (b) are identical with the corresponding zones in Kaimes Hill, and are best exposed in a small disused quarry near the western extremity of the Crag of Dalmahoy. There the basalt has a thickness of about 30 feet. Zone (c) is again marked by its pronounced columnar jointing, but segregation veins occur only sparingly, and the rock is on the whole somewhat coarser in grain than at Kaimes and Ravelrig. Zone (d) is a coarse dolerite with lenses and layers of dolerite-pegmatite, the latter being developed extensively in exposures along the dip slope of the highest crag. Zone (e), which is basaltic in texture, and zone (f), which is a coarse tholeiite, appear in occasional prominences near the base of the dip slope. The top of the sill is here concealed under the peat deposits which occupy the site of an old glacial lake.

The succession in Ravelrig Hill is the same as in Dalmahoy except that the lower basaltic zone is not seen east of Sheds's Quarry. Throughout this hill, however, zone (c), as in Kaimes Hill, is marked by its excessive development of segregation veins. The dolerite-pegmatites of zone (d) occur in the upper part of the south face of Ravelrig Quarry, and they may be studied in numerous crags to the west. The upper basaltic zone (e) outcrops more or less continuously, appearing to thicken towards the east end of the hill; it forms most of the south-eastern and south-western working faces of Hannahfield Quarry, and is well exposed in a prominent crag at the south-east end of the wood below the Lanark road. The highest coarse modification (f) passes locally into "white trap." The top of the sill is here obscured by drift deposits, and the contact with the overlying sediments has not been seen.

That the sill is a composite one is quite clear, but the order of injection of the constituent sheets is not always demonstrable. The lowest zone (a) shows distinct evidence of chilling in the occurrence of a tachylytic selvage well seen at the entrance of Ravelrig Quarry. The lower basalt (b) is everywhere clearly intrusive into (a), but does not show chilled margins; it contains numerous cognate xenoliths derived from (a). The upper basalt is richly charged with similar xenoliths, the abundance of which gives the rock at first sight the appearance of a fine-grained dolerite rather than a basalt. The relations between (c) and the other sheets are obscure, but at Kaimes Quarry and elsewhere are suggestive that (c) is the youngest

member of the complex. Probably (a), (d), and (f) all belong to the earliest injection, followed by (b) and (e) and later by (c). As will be seen from the detailed chemical and mineralogical

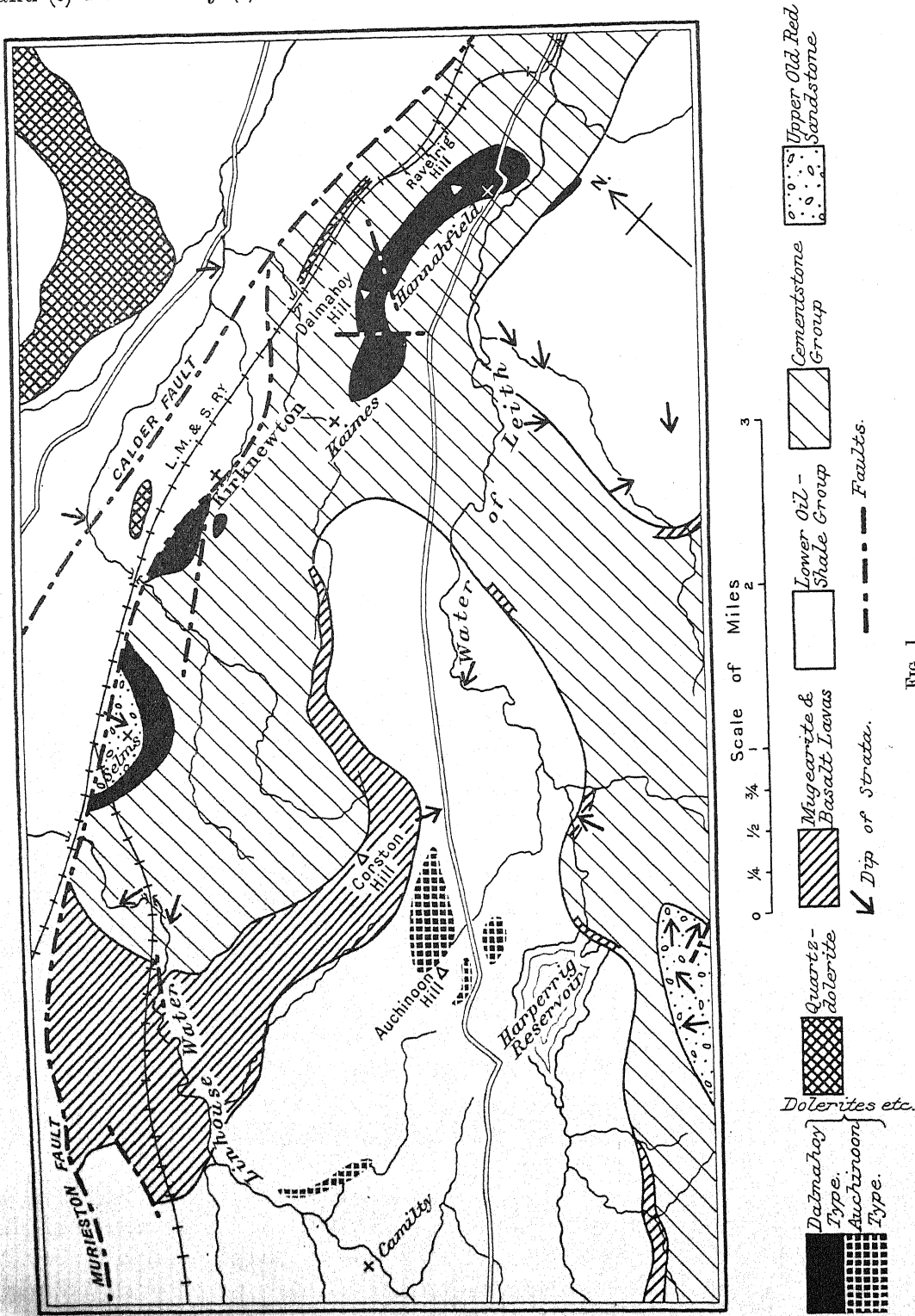


FIG. 1.

descriptions, the sheets show little variation in their bulk composition. The sill is built up by successive injections of very similar material.

A striking field character of all the rocks of the Dalmahoy intrusion is the marked change



of colour they undergo when first exposed. The freshly broken rocks are greenish grey in colour but darken quickly and become black on exposure to air. Along lines of open joints and on weathered surfaces generally the rocks are reddish brown. These colour changes are due to oxidation together with dehydration of chlorophæite, which is one of the chief rock constituents, and have been discussed in a paper in the *Mineralogical Magazine*.\*

No less distinctive are the segregation veins. These occur sporadically in most parts of the sill, but have their greatest development in the columnar sheet in Ravelrig and Kaimes Hills. Their colour is uniformly dull black. In thickness they range usually from mere films to about one-third of an inch, or exceptionally up to 3 inches. So abundant are they that in places one may count as many as fourteen within the space of a foot. Although anastomosis is not uncommon, the veins as a whole are at right angles to the dominant joint planes. On weathered surfaces they project as tiny ridges (see Pl. I, fig. 1).

Veins of secondary minerals occur occasionally along movement planes. For example, in the north face of Ravelrig Quarry a large calcite vein shows splendid crystals of "nail-head spar." In Kaimes Quarry a composite vein carries calcite, barytes, amethystine quartz, "chlorite," and occasional crystals of galena up to half an inch in diameter. Calcite and "chlorite" are the commonest vein minerals.

The underlying sediments, which belong to the Cementstone Group, are well exposed along the northern slopes of Kaimes Hill and Dalmahey Hill, with a dip to the south and south-east. A thin offshoot from the main sill near Kaimes Quarry, of interest chiefly because of its tachylytic borders, has been described and figured by T. CUTHBERT DAY,† who has also given an account of the instructive contact section at the entrance to Ravelrig Quarry.

*Johnsburn.*—Half a mile south-west of Balerno a small exposure of tholeiite of the Dalmahey type appears in the John's Burn immediately below the smithy. The rock is undecomposed, of coarse grain, and shows patches of fresh chlorophæite.

*Auchinoon.*—Three masses of dolerite have been mapped a short distance north of Harperrig Reservoir. The largest gives rise to the high ground of Auchinoon Hill and is entirely grass-grown except for a few decomposed knolls on the south-west slope. The second mass which occurs near the north side of the main road is the one which was described by MACLAREN.‡ It has attracted attention chiefly because of the interesting character of the overlying hornfelses which dip south at eighteen degrees. The contact phenomena have been described by Sir JOHN S. FLETT§ and by T. CUTHBERT DAY.|| The quarry, long disused, has been reopened recently. The igneous rock is a coarse-grained vesicular dolerite, dark green in colour, and for the most part in a highly decomposed condition. Vesicles and veinlets of chlorophæite and chloritic minerals are abundant, and it was these that were mistaken by MACLAREN for undigested fragments of "slate clay." The third occurrence is found on the south side of the road in the neighbourhood of Auchinoon. Here again the rock is everywhere extremely decomposed. The Auchinoon intrusions all occur near the base of the Lower Oil-Shale Group.

*Camilty.*—Along the right bank of the Linhouse Water, a quarter of a mile north of Camilty Mill, the upper part of an intrusive sill is exposed for some 16 yards with a maximum visible thickness of 3 feet. The rock is spheroidal, considerably decomposed, and overlaid by 12 feet of sandstone—the whole section dipping west-north-west at twenty degrees. Half a mile

\* *Loc. cit.*, p. 439.

† *Trans. Edin. Geol. Soc.*, 1920, vol. xi, p. 17.

‡ *Geology of Fife and the Lothians*, 1st ed., 1839, p. 171; and 2nd ed., 1866, p. 234.

§ "The Neighbourhood of Edinburgh," *Mem. Geol. Surv. Scotland*, 1910, pp. 314 and 315.

|| *Trans. Edin. Geol. Soc.*, 1920, vol. xi, pt. i, pp. 51-53; and 1923, vol. xi, pt. ii, pp. 128-130.

south-east of this point the sill is exposed in the Rae Burn and one of its tributaries. Here it is a moderately fresh dolerite, of coarse to medium grain, greenish-black colour, and shows abundant dull black patches of decomposed chlorophæite. One and a quarter miles south-east of Camilty, and a quarter of a mile south-west of Halfway House, a bore passed through an intrusive sill 257 feet thick which showed the megascopic characters of the Camilty rock. The top was proved 100 feet from the surface, and the bottom 400 feet above a prominent lava zone of unknown thickness.\* It is suggested that this intrusion may be correlated with the Camilty sill, and that the lava zone represents the Corston and Torweaving volcanic group.

*Red Craig.*—On both sides of the Linhouse Water, near the farm of Red Craig, Oakbank, a highly decomposed tholeiite sill forms crag features. On the right bank of the stream a splendid transgressive contact section is seen, but here, as elsewhere in the intrusion, the nature of the rock renders type determination impossible. Two extensions of the sill—hitherto considered “hard limey sandstones”†—are exposed in a small burn running north-west into the Linhouse Water. The main sill is truncated on the north by the Murieston fault.

*Selms.*—This sill, lying 1 mile south-south-east of Mid-Calder, forms a prominent semi-lunar ridge rising to over 700 feet at Selms Tops. Craggs are developed along the convex or north-west side, and the extremities of the ridge are truncated by the Murieston fault. From Selms Tops two low ridges extend westwards; the rock exposed at the extreme west end of the southern ridge is of coarse grain and greenish black in colour, and carries numerous small lenticles of chlorophæite. Horizontal segregation veins similar to those of Dalmahoy are sparingly developed. The freshest material was obtained from spheroidal blocks in the north ridge, that being the only locality where pyroxenes are preserved. Further east the sill has been quarried on a large scale at Gowanbrae. Here the rock is massive and intensely chloritised and shows a basal modification approaching “white trap.” Two hundred yards north-east of Gowanbrae Quarry a section shows vesicular tholeiite overlaid by a thin covering of sediments dipping east-south-east at ten degrees. Field evidence in this locality indicates a thickness for the sill of about 80 feet.

*Kirknewton.*—This mass may be considered an easterly extension of the Selms ridge. Trending east and west, it is about  $\frac{3}{4}$  mile in length and has an average dip south of twenty degrees. The central prominence of Hallcraigs (600 feet) has been quarried, and the summit exposures afford quite fresh material. Generally the rock is very similar to the chlorophæite-rich tholeiites of Dalmahoy, while locally there is a sparing development of the thin dark segregation veins so characteristic of that intrusion. Near this point a flooded quarry shows vertical columnar structure and typical thin, horizontal, anastomosing segregation veins. West of the Craigs a narrow and almost continuous outcrop extends down to Gogar Burn where the sill gives rise to a small waterfall. In this locality the rock is finer and less well preserved. A smaller mass at Overton Farm is separated from the main sill by a strike fault. A section on the south side of the farm-house shows a lower coarse modification in sharp unchilled contact with an upper finer modification, the former carrying abundant chlorophæite patches oxidised to a deep red colour.

The Selms and Kirknewton sills have been intruded near the base of the Cementstone Group.

#### IV. PETROLOGY.

A detailed study of their petrographical and chemical characters has shown that the intrusions belong to two distinct, though cognate, groups. The first includes the composite

\* Information obtained from records in Geological Survey Office, Edinburgh.

† Geological Survey 6-inch Map, Edinburghshire, Sheet 5, S.E.

sill at Ravelrig, Dalmahey, and Kaimes, together with the sills at John's Burn, Kirknewton, Overton, and Selms, all intruded at or near the base of the Cementstone Group and below the horizon of the Corston Hill lavas; the second comprises the Auchinoon sills, the Camilty sill, and the thick sill revealed by the bore near Halfway House, all of which occur a short distance above the lavas. The rocks of the first group show wide diversity of texture, ranging from basalts through medium-grained tholeiites to very coarse dolerites. They are all rich in chlorophæite, and all carry fayalite or pseudomorphs after that mineral. In their bulk composition they are closely related to the mugearites. The rocks of the second group are all dolerites, carrying much chlorite as well as chlorophæite, and in their chemical characters they are nearly related to the essexite \* of the Lochend sill. It is suggested that the chlorophæite-rich rocks with mugearitic affinities should be termed basalts, tholeiites, and dolerites of Dalmahey type, and that the dolerites rich in both chlorophæite and chlorites should be distinguished as dolerites of Auchinoon type.

#### A. THOLEIITES, DOLERITES, AND BASALTS OF DALMAHOY TYPE.

##### (a) THE RAVELRIG—DALMAHOY—KAIMES SILL.

The members of this composite sill show little variation in mineral composition, but several textural modifications are met with. For descriptive purposes the dominant rocks may be designated basalt, tholeiite (as defined by E. B. BAILEY † and H. H. THOMAS), and dolerite.

##### *Tholeiites.*

The tholeiites are fine-grained to medium-grained rocks consisting of moderately basic plagioclase, augite, fayalite, titaniferous magnetite, and apatite, together with a varying amount of intersertal glassy or felsitic mesostasis which is invariably associated with much chlorophæite and frequently carries primary quartz.

*Early Constituents.*—The dominant early constituent is plagioclase, which makes up 46 to 48 per cent. of the rock. The crystals average about 0.5 mm. although they occasionally attain a length of over 1 mm. They are twinned on the Carlsbad and Albite laws, rarely on the Pericline law, and show well-marked zonal structure. They are almost free from inclusions, only an occasional small apatite inclusion having been noted. Measurements of refractive indices and extinction angles indicate a range of composition from acid labradorite to oligoclase, but the bulk of the felspar has a mean refractive index near 1.5546, which indicates a basic andesine with composition approaching  $Ab_{56.5}An_{43.5}$ . The felspar crystals are occasionally bent.

Augite, which makes up from 12 to 15 per cent. of the rock, is a pale brown variety, not usually pleochroic. It occurs partly in anhedral plates showing a sub-ophitic relation to the feldspars, partly in columnar crystals with prismatic habit which attain a maximum length of 1.5 mm. and breadth of 0.25 mm. Quite frequently the crystals show simple or lamellar twinning parallel to 100. Like the augite of the quartz-dolerites of West Lothian, they carry large crystals of magnetite as peripheral inclusions. Fluid inclusions occur fairly often in the central parts of the crystals. The columnar augites are often curved or otherwise distorted, a phenomenon which, as E. B. BAILEY and H. H. THOMAS ‡ have pointed out, is of

\* "The Geology of the Neighbourhood of Edinburgh," *Mem. Geol. Surv.*, 1910, p. 292.

† "Tertiary and Post-Tertiary Geology of Mull," *ibid.*, 1924, p. 280.

‡ *Op. cit.*, p. 303.



common occurrence when crystallisation from a sub-basic magma was accompanied by separation of an acid residuum.

The olivine of the tholeiites is almost completely replaced by chlorophæite, but determinations by a Berek compensator of the values of the double refraction of small unaltered patches gave values up to 0.048, showing clearly that, like the fresher olivines of the associated basalts, it is a variety very rich in iron and approaching fayalite. The fayalite is of late crystallisation. It is moulded on both feldspar and augite, and most of the crystals, which are commonly markedly euhedral, occur in association with patches of glassy mesostasis.

Iron oxides, in the form of crystals and skeletal growths, are abundant, making up from 6 to 7 per cent. of the rock. There may be some ilmenite, but the bulk of the iron ore has the characters of titanomagnetite. Its crystallisation began during the growth of the augites and was continued during the period of consolidation of the mesostasis.

*Mesostasis.*—The intersertal mesostasis, which makes up nearly 30 per cent. of the average rock, can be resolved into two sharply separated phases, the first consisting of glass or devitrified glass with microlites, and the second consisting mainly of chlorophæite (see Pl. II, fig. 3). In the glassy part of the mesostasis the chief element in some cases is a pale brown glass, but very often the place of the glass is taken in large measure by a feldspathic "cement," probably poorly differentiated orthoclase. Included in the glass are numerous microlites and acicular crystals of albite-oligoclase and augite. Apatite is usually abundant, this mineral being mainly of late crystallisation. And in keeping with the late concentration of iron, characteristic of the rocks, we find an abundant development of granules and skeletal rods of magnetite and small hexagonal plates of hæmatite. Sometimes, too, the glassy mesostasis contains chlorophæite pseudomorphing narrow elongated laths whose shapes suggest original skeletal olivines. Small patches of quartz occur occasionally, and very rarely pseudospherulites which may represent fine cryptographic growths of quartz and feldspar.

As determined by micrometric measurements the tholeiites carry from 10 to 15 per cent. of chlorophæite. Some of the chlorophæite, as we have seen, replaces fayalite crystals or skeletal growths associated with the glassy mesostasis, and some occurs interstitially. The bulk of the mineral, however, is found in the form of amœboid patches occupying usually a central position in the areas of glassy mesostasis. Occasionally the larger patches of chlorophæite have a central area of carbonates.

The fine- to medium-grained tholeiites described above, and characterised also by the unusual habit and abundance of their segregation veins, constitute the major part of the highly columnar portion of the sill. Tholeiites of coarser grain form a persistent zone at the base of the sill and also occur as *schlieren* in the finer tholeiites. The most striking macroscopic character of these coarse-grained tholeiites is the abundance and unusually large size of the patches of chlorophæite. The feldspars of early crystallisation attain an average length of 1 mm., and most of the augite is in anhedral plates in subophitic relation to the former. Not infrequently the augite is in part replaced by a green mica-like mineral with strong double refraction (? bowlingite). The glassy mesostasis is in somewhat greater amount than in the finer tholeiites. The amœboid patches of chlorophæite are often separated from the glass by a fringe of pale green chlorite which also occurs as spherules in the chlorophæite.

For a distance of about 10 feet upwards from the tachylytic selvage at the base of the sill the lowest member of the complex, a coarse tholeiite, has been highly altered, the dark tholeiite passing gradually downwards into a rock which is grey on fresh fracture and weathers with a yellow or yellow-brown crust. In thin slices it is seen that the change has been brought about by the introduction of carbonic acid. The augite of these "white traps" is almost

completely replaced by rhombohedral carbonates, but most of the felspar is unaltered or has undergone only slight carbonisation. No original chlorophæite is left, its place being taken by carbonates together with chalcedony and a pale yellow to colourless isotropic substance with refractive index approximately 1.47 and soluble in caustic alkalies—probably opaline silica. Much leucoxene has resulted from the partial alteration of the titaniferous magnetite, and in some cases there is a considerable development of hæmatite at the expense of the same mineral. The accessory apatite and hæmatite remain unaltered. The selvages of tachylite consist of a black glass with numerous small phenocrysts, all of which appear to be altered felspar.

#### *Dolerites.*

The dolerites are coarser grained than the normal tholeiites, the average length of the early felspars being about 1 mm. They differ from these tholeiites also in that the augite does not so often assume a columnar habit, most of it being in anhedral plates in subophitic relation to the felspars. In this respect the dolerites resemble the coarser tholeiites, but they are distinguished from the latter by the much more mature crystallisation of the intersertal mesostasis (see Pl. II, fig. 4). Glass is absent, and the mesostasis is seen to be dominantly feldspathic, consisting largely of acicular crystals and skeletal growths of albite-oligoclase set in a matrix of untwinned orthoclase. It contains also occasional acicular crystals of augite. Hæmatite and magnetite are less abundant than in the tholeiites. Euhedral fayalites pseudomorphed by chlorophæite occur occasionally. Much of the chlorophæite, as in the tholeiites, is in the form of large amœboid patches associated with the intersertal mesostasis, but the crystalline character of the latter has led to a less distinct separation than in the glassy tholeiites, and a good deal of the chlorophæite may be described as interstitial, occupying the interstices between the felspar laths of the matrix. An occasional euhedral, pale brown hornblende occurs in the areas of chlorophæite. A small amount of quartz occurs interstitially. Apatite, frequently in skeletal form, is abundant in the mesostasis.

Found only in association with the dolerites, which immediately overlie the columnar tholeiites, are lenses and persistent layers of from 1 to 2 feet in thickness of an exceptionally coarse rock, which, in comparison with the normal dolerites, may be termed dolerite-pegmatite. Numerous exposures of these pegmatites occur from Ravelrig Quarry westwards as far as the extreme west of Dalmahey Hill. Their most conspicuous character in hand specimen is an unusual mode of occurrence of chlorophæite. The amœboid areas are unusually large—one exceptional patch measured 5 by 1 cm., but much of it occurs in variously orientated groups of thin parallel rods (see Pl. I, fig. 2). The longest rods are 2.5 cm. in length and 0.5 mm. in width and thickness. The majority range from 1 to 1.5 cm. in length. The unusual coarseness of these rocks is shown also by the size of the glistening cleavage surfaces of the felspars, which are tabular in habit and attain a maximum length of 1.6 cm. Their average length is about 5 mm.

In thin section the rocks show a number of interesting features. All the augite of early crystallisation is in graphic intergrowth with plagioclase (see Pl. I, fig. 6), and additional proof of the early crystallisation of the latter is seen in the fact that the graphic intergrowth with augite is confined to the marginal portions of the larger felspars. This graphic intergrowth of augite and plagioclase recalls the similar occurrence in "coarsely crystalline masses and veins" in the dolerite of Hailstone Hill, Rowley, Staffordshire, described and figured first by ALLPORT\* and afterwards by Sir J. J. H. TEALL.† The large felspars are strongly

\* *Quart. Journ. Geol. Soc.*, vol. xxx, 1874, p. 549, and pl. xxxiv, fig. 28.

† *British Petrography*, 1888, p. 212, and pl. xxiii, fig. 2.

zoned, the central portion of finely zoned andesine usually sharply separated from a distinct outer zone of oligoclase. The augite is sometimes non-pleochroic, sometimes faintly pleochroic in the purplish-brown tints which indicate high titanium content; it is unusually rich in fluid inclusions. Euhedral pseudomorphs of chlorophæite after fayalite are found particularly near the margins of areas of mesostasis (see Pl. I, fig. 5).

In keeping with the coarser-grained character of the rocks, the mesostasis of the pegmatites is coarser than that of the associated dolerites. The feldspar includes albite-oligoclase in untwinned laths and as skeletal outgrowths from the margins of the large feldspars and also orthoclase. The augite occurs similarly, partly as skeletal outgrowths in optic continuity with the augite of the graphic augite-feldspar groups, partly as isolated needles and forked prisms. The euhedral titaniferous magnetite of the early crystallisation gives place to bars, often arranged in parallel fashion over considerable areas and normal to the length of the chlorophæite rods (see Pl. I, fig. 4). The latter are not veinlets as we suggested in an earlier paper.\* They are bounded by crystallographic outlines, and recall in shape and in proportions as well as in transverse fractures the skeletal olivines described and figured by Professor J. D. DANA † from the basalts of Mauna Loa and Kilauea. They are, however, very much larger. They are comparable in size with the fayalites of certain fayalite-magnetite slags described by Professor J. H. L. VOGT, ‡ which vary in length from 1.5 to 2 cm. and in breadth from 0.5 to 1 mm. They have the rod-like habit of the specimens from the Hawaiian islands rather than the tabular habit of the fayalite of the slags. Not unfrequently the chlorophæitisation of the fayalites has been accompanied by a sporadic development of pale brown hornblende, which occurs sometimes fringing the pseudomorphs, sometimes as euhedral crystals enclosed in the chlorophæite. A similar late growth of euhedral brown hornblende is seen also in the large amoeboid patches as well as in the interstitial chlorophæite. The chlorophæite is accompanied sometimes by a fair amount of quartz. Six-sided scales of hæmatite and skeletal plates of the same mineral are found, though not so abundantly as in the tholeiites. Apatite is a constant constituent and is often in great abundance. Like all the minerals of the mesostasis, except orthoclase and quartz, it shows a strong tendency to take the form of skeletal crystals.

#### *Basalts.*

The basaltic modifications occur in two positions—near the base and near the top of the sill. They are distinguished by their finer-grained texture and by the presence of numerous cognate xenoliths derived from the earlier doleritic and tholeiitic types (see Pl. II, fig. 2). They are noteworthy also in that they carry much more unaltered fayalite than the coarser varieties of rock.

The larger constituents include isolated crystals of pale brown augite, zoned andesines, averaging about 0.7 to 0.8 mm. in length, and crystals of titaniferous magnetite. For the most part, however, the above minerals, together with fayalite, are grouped as glomeroporphyritic aggregates which are of the nature of cognate xenoliths. The augite, which has the usual marginal inclusions of magnetite, is in subophitic relation to the feldspar, and the bending of the augite crystals is very pronounced. The andesines often show corroded margins where they are in contact with the groundmass. The fayalite, which is largely replaced by chlorophæite, is often moulded on, very rarely is it partly enclosed in, the outer

\* *Min. Mag.*, vol. xx, 1925, p. 436.

† *Characteristics of Volcanoes*, 1890, pp. 324–326.

‡ "Über die Mineralbildung in Silikatschmelzlösungen," *Videnskabs-Selskabets Skrifter. I. Math.-naturv. Klasse.*, 1903, p. 112.



margins of the augite crystals. It is sometimes euhedral, sometimes rounded. The average longest diameter of the fayalite is about 0.4 mm. The smallness of the unaltered patches of the olivines (although they are larger than in the tholeiites and dolerites) presents difficulties in the way of satisfactory determination of their optical properties (see Pl. II, fig. 6). The maximum double refraction, as determined by a Berek compensator, is 0.049. A determination of the refractive index by the immersion method, in which we were assisted by Mr D. BALSILLIE of the Royal Scottish Museum, gave a value for  $\beta$  of 1.77. The axial angle is fairly large. The data point to the olivine being a variety exceptionally rich in iron, and the term "fayalite" has been used throughout the paper to denote such olivines.

The groundmass of the basalts consists of oligoclase, orthoclase, augite, fayalite, iron ores, chlorophæite, and apatite, with sometimes a little glass. Most of the felspar is in the form of laths of oligoclase. A gradation is met with from the phenocrystic felspars with lengths of 0.7 to 0.8 mm. downwards, but the majority of the groundmass felspars average 0.2 to 0.3 mm. in length in the lower basalts and 0.4 mm. in the upper. The augite is granular, the diameter of the grains ranging from 0.05 to 0.1 mm. in rocks of varying texture. A feature of the basalts is the somewhat variable but often abundant development of small, frequently unaltered, fayalites in the groundmass. These are often euhedral and range up to 0.1 mm. in length. Here also, as in the coarse-grained rocks, there is much magnetite and apatite of late crystallisation. The above minerals are associated with minute interstitial patches, sometimes of orthoclase, sometimes of green chlorophæite, the two types occurring together in the same slice. Occasionally the oligoclases of the groundmass show a rude fluxional arrangement. A distinctive feature of the basalts, particularly of those of the upper zone, is the relatively large content of pale brown amphibole of late origin and usually associated with patches of chlorophæite. Interstitial quartz occurs sporadically, but never in large amount, and one slice from the upper zone was exceptional in carrying very fine graphic intergrowths of quartz and felspar.

#### (b) RELATED INTRUSIONS.

The specimens sliced from the larger intrusion at Kirknewton are all tholeiites, those from Hallcraigs being identical with the coarse chlorophæite-rich tholeiites at Ravelrig, while elsewhere the rocks in composition and texture are comparable with the normal tholeiites described above. From the Overton mass have been obtained both the normal and the coarse-grained tholeiites (see Pl. II, fig. 5) and also basalts similar to those of the upper zone at Dalmahey. Specimens from different parts of the large intrusion at Selms are all comparable with the dolerites of Dalmahey, but many of them are highly altered. The rocks at Red Craig are so decomposed that comparison with other rocks is difficult, but in all probability they were originally tholeiites of the Dalmahey type.

#### (c) DISTINCTIVE MINERALOGICAL AND CHEMICAL CHARACTERS OF THE THOLEIITES, BASALTS, AND DOLERITES OF DALMAHOY TYPE.

When compared with other basic intrusions associated with the Carboniferous strata of the Edinburgh district, the suite of rocks just described presents certain rather distinctive features. One notes, for example, the moderately basic character of the plagioclase, the iron-rich nature of the olivine, together with its occurrence along with primary quartz, and the remarkable abundance of chlorophæite. The order of crystallisation of the minerals is also noteworthy. As in the case of the basalts from Franz Josef Land described by NEWTON

chlorophane  
gonal plates  
fairly wide  
oligoclase  
the average  
for the dolerite  
rock. Quartz  
veins and  
material  
occurs as  
laths some-  
times enclosed  
traverse the  
least of the  
arrangement  
being inter-

as led to "the formation of a mother-liquor poor in silica and alumina and rich in iron may add, in water. In all the varieties of our rocks the first mineral to crystallise is plagioclase (acid labradorite or basic andesine), followed by augite. In the dolerite-pegmatites there was a period of simultaneous crystallisation of andesine and augite towards the end of the period of augite growth does the magnetite make its appearance. The last of the early constituents to crystallise was fayalite. The late concentration of iron is seen again in the unusual abundance of magnetite and hæmatite in some of the tholeiites and dolerites, of those accompanied by skeletal fayalites in the pegmatites, and of fayalite in the groundmass of the basalts. But perhaps the most striking evidence of the late concentration is seen in the chlorophæite, which, in our opinion, represents the final highly differentiated aqueous mother-liquor of the rocks and which is shown in analysis E of Table I. We would emphasise here the fact that the chlorophæite does not represent palagonitised or chlorophæitised glassy mesostasis, nor is it derived from the augites.† There is always a sharp boundary between glass and chlorophæite and usually the same slice shows numerous areas which are completely glassy and others which consist entirely of chlorophæite. The augite of the fresh rocks shows no evidence of alteration. In the few cases when it does it is replaced, not by chlorophæite but by (?) bowlingite. We regard the chlorophæite as a primary constituent, its mode of occurrence with the analcite of the teschenites. A primary origin is suggested by O. O. BAKLUND ‡ (H. G. BACKLUND) for a colloidal chloritic substance, which resembles hullite, occurring in amygdules and in the mesostasis of a basalt described by S. I. TOMKEIEFF § for chlorites in certain basaltic Carboniferous rocks. Some of the chlorophæite of the Dalmahoy rocks replaces fayalite. In all cases it is also a primary occurrence, the fayalite having been hydrated during the devolatilisation of the rock.

which witness to the great concentration of water during the last stages of the crystallisation and the abundance of hæmatite in the mesostasis of most of the rocks, and the presence of brown hornblende, particularly in the upper basalt zone. The same factors account for the rapid crystallisation in the mesostasis of the dolerite-pegmatites by the pronounced skeletal-growth forms of most of the constituents.

The mineral characters of the rocks are given in the first three analyses in Table I. In the analysis of a typical tholeiite from Ravelrig Quarry (I) we owe to the kindness of Mr. J. W. LUNN. It is remarkably similar to the analysis of a dolerite from Dalmahoy (II) by J. W. LUNN and REID,|| and these two analyses may be taken as representative of the rocks of the Ravelrig-Dalmahoy-Kaimes intrusion. Analysis III, which represents a modification with some cognate xenoliths, departs from the normal composition by containing unusually high alumina. On comparing the analyses with those of other dolerites, one notes particularly the low magnesia and lime, the high total iron, and the unusually high percentage of water. Their nearest equivalents among Carboniferous igneous rocks are the mugearitic lavas such as (C) and (D) of the Mull of Galloway, the mugearitic character of the intrusions is also well seen if they are compared with the "mugearitic mugearites" of Canna and Rum, (A) and (B) of Table I, described by

*Geol. Soc.*, vol. liii, 1897, p. 487.

WADIA, "Palagonite-bearing Dolerite from Nagpur," *Rec. Geol. Surv., India*, vol. lviii, 1925, p. 342; and the Basaltic Lavas penetrated by the deep boring for Coal at Bhusawal, Bombay Presidency," *ibid.*, p. 133.

Bolshezemelsk tundra," *Trav. Musée Géol. Pierre le Grand, Acad. Sci. St Pétersburg*, vol. iv, 1911, pp. 75-97. *ibid.*, l. xxi, 1926, pp. 73-82.

STON, "Chemical Analyses of Igneous Rocks," *U.S. Geol. Surv., Prof. Paper*, 99, 1917, p. 888.

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Mr T. C.  
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Dr HARKER \* in "The Geology of the Small Isles of Inverness-shire." It may be observed also that the analyses of the Ravelrig and Dalmahoy rocks correspond well with the mugearite magma-type in the variation-diagram for the Tertiary alkaline magma-series of Mull.†

TABLE I.

	I.	II.	III.	A.	B.	C.	D.	E.
SiO <sub>2</sub>	52.90	51.37	52.60	49.92	50.70	50.06	50.24	32.95
TiO <sub>2</sub>	2.35	3.09	1.70	2.04	1.89	2.46	3.09	0.62
Al <sub>2</sub> O <sub>3</sub>	13.02	13.27	16.32	12.83	14.60	15.72	15.01	5.40
Cr <sub>2</sub> O <sub>3</sub>	..	..	..	trace	n.d.	..	..	..
V <sub>2</sub> O <sub>5</sub>	..	..	..	0.04	n.d.	..	..	..
Fe <sub>2</sub> O <sub>3</sub>	6.62	5.12	5.34	6.96	5.23	3.94	8.94	12.37
FeO	6.31	7.59	6.12	6.21	7.68	7.63	6.46	9.18
MnO	..	trace	0.34	0.52	0.42	0.30	..	0.33
(Co,Ni)O	..	0.02	..	0.03	tr. Ni	0.03	..	..
MgO	2.86	2.83	3.61	3.78	4.15	3.82	3.16	4.75
CaO	6.37	6.83	6.39	7.25	7.20	5.90	5.61	3.05
SrO	..	0.02	..	trace	trace	..	..	..
BaO	..	0.26	..	0.09	0.08	0.03	..	..
Na <sub>2</sub> O	3.51	3.58	3.10	3.72	3.71	4.55	3.47	1.68
K <sub>2</sub> O	2.00	1.85	1.55	1.73	1.33	2.16	1.91	0.36
Li <sub>2</sub> O	..	..	..	trace	trace ?	nt. fd.	..	..
H <sub>2</sub> O+105°	} 3.73	} 2.28	1.32	1.05	1.15	1.36	1.77	5.20
H <sub>2</sub> O at 105°			0.90	3.58	2.08	0.67	1.05	23.90
P <sub>2</sub> O <sub>5</sub>	0.90	0.43	0.64	0.45	0.49	0.64	..	..
CO <sub>2</sub>	..	1.80	nil	..	..	1.08	..	..
Cl	..	0.03	..	..	..	0.04	..	..
S'	..	trace	..	trace ?	..	..	..	..
FeS' <sub>2</sub>	..	..	..	..	..	nt. fd.	..	..
	100.57	100.37	99.93	100.20	100.71	100.39	100.71	99.79

- I. Tholeiite, Ravelrig Quarry. Anal. T. CUTHBERT DAY.  
 II. Dolerite, Dalmahoy Hill. Anal. HARRISON and REID. Quoted from *Chemical Analyses of Igneous Rocks*, by H. S. WASHINGTON, 1917, p. 888.  
 III. Basalt, Dalmahoy Hill. Anal. W. H. HERDSMAN.  
 A. Doleritic mugearite, Eilean a' Bhaird, Canna. Anal. W. POLLARD. Quoted from "Geology of the Small Isles of Inverness-shire," *Mem. Geol. Surv.*, by A. HARKER, 1908, p. 130.  
 B. Doleritic mugearite, Pass S. of Fionn-Chrò, Rum. Anal. E. G. RADLEY. Quoted from "Geology of the Small Isles of Inverness-shire," *Mem. Geol. Surv.*, by A. HARKER, 1908, p. 130.  
 C. Basaltic mugearite, Fintry Hills. Anal. E. G. RADLEY. Quoted from "Geology of the Glasgow District," *Mem. Geol. Surv.*, 1925, p. 182.  
 D. Mugearite, Creag a' Mhara, S. Bute. Anal. J. V. HARRISON. Quoted from W. R. SMELLIE, *Trans. Geol. Soc. Glasg.*, vol. xv, part iii, 1916, p. 359.  
 E. Chlorophaeite, Ravelrig Quarry. Anal. W. H. HERDSMAN. Quoted from R. CAMPBELL and W. J. LUNN, *Min. Mag.*, vol. xx, 1925, p. 438.

#### (d) THE SEGREGATION VEINS.

Segregation veins are found in association with all the textural modifications of the mugearitic intrusions, but occur in unusual abundance (see Pl. I, fig. 1) in the tholeiites, where the smaller veinlets can sometimes be demonstrated to be continuous with the larger patches of intersertal mesostasis. In mineral composition they are closely related to the mesostatic parts of the parent rocks. They consist mainly of albite-oligoclase, orthoclase, quartz, and

\* *Op. cit.*, *Mem. Geol. Surv.*, 1908, pp. 130-131.

† "Tertiary and Post-Tertiary Geology of Mull," *ibid.*, 1924, p. 26.



chlorophæite. Needle-like crystals of brown augite, granules and bars of magnetite, hexagonal plates of hæmatite and apatite are present in varying amounts. The veins show a fairly wide range of texture. In examples of coarser-grained veins the larger feldspars (albite-oligoclase) may average 0.7 mm. in length; in the finer veins, which are much more numerous, the average length of the large feldspar laths is about 0.2 mm. There is a distinct tendency for the degree of coarseness of the veins to vary with the coarseness of the associated parent rock. Quartz, occurring in micropoikilitic relation to the feldspar, is abundant in the coarser veins and seldom seen in the finer veins, being concealed probably in the microfelsitic material of the latter. All the veins carry interstitial chlorophæite, and this mineral also occurs as larger patches in which microspherulitic structure is a common feature, feldspar laths sometimes acting as nuclei for the spherulites. Euhedral quartzes are occasionally enclosed in the chlorophæite, and veinlets proceeding from larger areas of the latter mineral traverse the quartz of the micropoikilitic quartz-feldspar association, showing that some at least of the quartz is earlier than the chlorophæite. Exceptionally there is a good fluxional arrangement of the feldspars. Vesicular structure is of infrequent occurrence, the vesicles being infilled with chlorophæite, sometimes with a central patch of carbonates.

TABLE II.

	I.	A.	B.
SiO <sub>2</sub>	65.46	69.57	66.27
TiO <sub>2</sub>	0.48	0.65	0.87
Al <sub>2</sub> O <sub>3</sub>	11.90	13.03	11.92
Fe <sub>2</sub> O <sub>3</sub>	5.09	0.98	3.09
FeO	2.96	3.59	3.18
MnO	n.d.	n.d.	0.31
(Co,Ni)O	n.d.	n.d.	nt. fd.
MgO	1.27	1.06	1.44
CaO	1.67	1.56	3.30
BaO	n.d.	n.d.	nt. fd.
Na <sub>2</sub> O	3.95	4.57	2.89
K <sub>2</sub> O	4.39	2.37	4.03
Li <sub>2</sub> O	n.d.	n.d.	trace.
H <sub>2</sub> O+105°	3.24	2.04	{ 1.51
H <sub>2</sub> O at 105°			
P <sub>2</sub> O <sub>5</sub>	0.22	0.47	0.17
CO <sub>2</sub>	n.d.	0.70	0.53
FeS <sub>2</sub>	n.d.	n.d.	nt. fd.
	100.63	100.59	100.29

I. "Segregation Vein" in Tholeiite, Ravelrig Quarry. Anal. T. CUTHBERT DAY.

A. "Segregation Vein" in Quartz-dolerite, North Queensferry. Anal. T. CUTHBERT DAY. *Trans. Edin. Geol. Soc.*, vol. xii, 1927.

B. Cragdurite (acid), Allt an Dubh-choire, Mull. Anal. E. G. RADLEY. "Tertiary and Post-Tertiary Geology of Mull," *Mem. Geol. Sur.*, 1924, p. 19.

The chemical composition of a typical segregation vein, kindly analysed for us by Mr T. CUTHBERT DAY, is given in Table II. Compared with the segregation veins of quartz dolerites the veins of the Dalmahoy complex are poorer in silica, much richer in alkalis, particularly in potash, and notably richer in iron oxides. The more alkaline character is in keeping with the mugearitic affinities of the parent rocks, and the high content of iron oxides gives further evidence of the late concentration of iron. The veins in some respects, both

mineralogically and texturally, recall the acid craignurites \* of Mull, but, as will be seen from the analyses in Table II, they are poorer in lime and richer in iron oxides and alkalies. Sir JOHN F. FLETT † has shown that the segregation veins of the quartz dolerites and teschenites have mineralogical peculiarities which indicate that they have come from the same magmas as the rocks which they intersect. The evidence for co-magmatic origin is equally clear in the case of the mugearitic intrusions and their segregation veins. Not only are the latter different from the segregation veins of the quartz dolerites and teschenites in their detailed mineralogical and chemical character, their dull black colour gives a ready means of distinguishing them in the field.

#### B. DOLERITES OF AUCHINOON TYPE.

The rocks of the Auchinoon and Camilty intrusions and the specimens from the thick sill revealed by the deep bore near Halfway House are all dolerites. They are for the most part coarse-grained, the feldspars of the Auchinoon rocks attaining a maximum length of 4 mm. Not infrequently they are highly vesicular. They are markedly ophitic (see Pl. II, fig. 1), and feldspathic mesostasis is in small amount or entirely absent. Only locally, as at Rae Burn, where the augites sometimes tend to be columnar in habit and where the rock contains a fair amount of feldspathic mesostasis, do we find rocks approaching the Dalmahoy dolerites in texture.

The augite is pale brown in colour and sometimes shows basal lamination; the only inclusions are fluid cavities, and the mineral rarely shows any trace of decomposition. The feldspar in most of the slices is highly albitised, a feature which has not been noted in rocks of the Dalmahoy type. No fresh olivine has been observed, but chlorophæite and chlorite occur in occasional pseudomorphs after that mineral. Large skeletal plates of titaniferous magnetite of late crystallisation are of frequent occurrence, and apatite is a common accessory. All the slices are rich in intersertal amoeboid patches of green and brown chlorophæite and colloform chlorites, and the same minerals occur everywhere interstitially. In the larger patches there is often a central area of scaly pleochroic delessite. The vesicles are circular in section, often bounded by tangential feldspar laths, and are infilled usually with chlorite—rarely the centre of a vesicle is occupied by carbonates. The chlorophæite and chlorites, as in the case of the rocks of Dalmahoy type, are regarded as products of the primary consolidation of the dolerites. The tachylyte selvage of the Camilty sill shows an incipient development of variolitic structure.

An analysis of the Auchinoon dolerite by Mr T. CUTHBERT DAY is quoted in Table III. Comparing it with the analysis of the typical mugearitic tholeiite of Ravelrig we find that it has lower silica, much higher magnesia, and a much more marked preponderance of soda over potash. The high soda of the Auchinoon rock corresponds with the albitised character of its feldspars, and the low potash may be accounted for by the paucity of the feldspathic mesostasis which carries the orthoclase of the Ravelrig and Dalmahoy rocks. The higher magnesia of the Auchinoon dolerite finds mineralogical expression in the very large development of chlorites accompanying the chlorophæite and in a somewhat larger proportion of augite. Although dissimilar in mineralogical characters, the Auchinoon rock has striking chemical affinities with the dolerite of the Lochend sill (Analysis II, Table III), regarded by Sir JOHN S. FLETT ‡ as nearly related to the essexites.

\* "Tertiary and Post-Tertiary Geology of Mull," *Mem. Geol. Surv.*, 1924, p. 19.

† "The Neighbourhood of Edinburgh," *ibid.*, 1910, pp. 298 and 307.

‡ *Ibid.*, 1910, pp. 292-3.

TABLE III.

	A.	B.	C.
SiO <sub>2</sub>	48.52	48.63	52.90
TiO <sub>2</sub>	1.73	2.04	2.35
Al <sub>2</sub> O <sub>3</sub>	13.07	15.03	13.02
Fe <sub>2</sub> O <sub>3</sub>	5.22	0.51	6.62
FeO	7.85	9.55	6.31
MnO	0.49	0.20	..
(Co, Ni)O	..	nt. fd.	..
MgO	7.21	6.34	2.86
CaO	5.89	5.95	6.37
SrO	..	n. d.	..
BaO	..	0.04	..
Na <sub>2</sub> O	5.29	5.32	3.51
K <sub>2</sub> O	0.74	0.56	2.00
Li <sub>2</sub> O	..	trace	..
H <sub>2</sub> O+105°	2.99	3.16	} 3.73
H <sub>2</sub> O at 105°	1.48	0.93	
P <sub>2</sub> O <sub>5</sub>	0.30	0.34	0.90
CO <sub>2</sub>	0.07	1.12	..
FeS <sub>2</sub>	..	0.44	..
Cl	trace	..	..
	100.85	100.16	100.57

- A. Dolerite, Auchinoon. Anal. T. CUTHBERT DAY. Quoted from T. C. DAY, *Trans. Edin. Geol. Soc.*, vol. xi, part ii, 1923, p. 129.
- B. Essexite, Lochend, near Edinburgh. Anal. E. G. RADLEY. Quoted from "Geology of Neighbourhood of Edinburgh," *Mem. Geol. Sur.*, 1910, p. 293.
- C. Tholeiite, Ravelrig Quarry. Anal. T. CUTHBERT DAY.

## V. THE AGE OF THE INTRUSIONS.

The Dalmahoy complex and the allied sills have all been intruded at or near the base of the Cementstone Group (see map, fig. 1). The dolerites of Auchinoon type occur a short distance above the Corston Hill lava zone—that is, near the base of the Lower Oil-Shale Group; and the essexites of the Lochend and Hawkhill sills, it may be noted, occupy a similar position relative to the lavas of the Arthur's Seat volcano. The Selms and Kirknewton sills are truncated by the Murieston fault, showing that the intrusions are older than the Permian-Carboniferous movements. There can, therefore, be no doubt that this suite of cognate intrusions is of Carboniferous age. Two further facts, however, lead us to regard them as belonging to a very early stage of the Carboniferous: (a) they occur along the strike of the belt of mugearitic lavas with which they have obvious affinities; (b) investigation has shown that similar rock types do *not* occur in any of the numerous intrusions north of the Murieston fault where the associated strata belong to higher horizons in the Carboniferous system. We regard the mugearitic and essexitic intrusions of the Dalmahoy syncline as hypabyssal expressions of the magma which gave rise to the accompanying effusive mugearites and allied basalts.

## VI. ACKNOWLEDGMENTS.

We wish to take this opportunity of thanking Mr T. CUTHBERT DAY, F.R.S.E., who has done so much to advance our knowledge of the chemical characters of the igneous rocks of



the Lothians, for his great kindness in analysing the tholeiite and associated segregation veins of Ravelrig Quarry. To Mr R. M. CRAIG, M.A., B.Sc., we are indebted for assistance in the photographic part of the work. We have to thank Mr MURRAY MACGREGOR, Assistant Director of the Geological Survey, for kindly giving us the opportunity of examining specimens and sections of rocks from the bore at Halfway House. Grateful acknowledgment is due also to the Carnegie Trust for a grant to defray expenses incurred in the preparation and reproduction of the illustrations.

## EXPLANATION OF PLATES.

## PLATE I.

Fig. 1. Segregation veins in columnar tholeiite at Ravelrig Quarry.

Fig. 2. *Dolerite-pegmatite*. Ravelrig Quarry. The black bars are chlorophæite replacing skeletal fayalites. Reflected light.  $\times 4\frac{1}{2}$ .

Fig. 3. *Tholeiite of Dalmahoy Type*. Ravelrig Quarry. The larger black areas are all chlorophæite, partly replacing fayalite, but chiefly in irregular patches. Intersertal glassy mesostasis is abundant. Other constituents are andesine, augite, and titanomagnetite. Ordinary light.  $\times 9$  diameters.

Fig. 4. *Dolerite-pegmatite*. Ravelrig Quarry. The narrow lath-like bodies crossing diagonally from the top right-hand corner are chlorophæite pseudomorphs after skeletal fayalite. Note also skeletal bars of titanomagnetite arranged normal to the fayalite pseudomorphs. Ordinary light.  $\times 9$  diameters.

Fig. 5. *Dolerite-pegmatite*. Ravelrig Quarry. Shows euhedral pseudomorphs of chlorophæite after fayalite in the mesostasis of the rock, and large crystals of andesine bordered by oligoclase. Ordinary light.  $\times 20$  diameters.

Fig. 6. *Dolerite-pegmatite*. Ravelrig Quarry. Shows mode of occurrence of most of the augite, namely, in graphic intergrowth with andesine. Ordinary light.  $\times 20$  diameters.

## PLATE II.

Fig. 1. *Dolerite of Auchinoon Type*. Camilty Sill. Shows the characteristic ophitic relation of augite and plagioclase. The dark intersertal material is partly chlorophæite, partly colloform chlorites. Ordinary light.  $\times 20$  diameters.

Fig. 2. *Basalt of Dalmahoy Type*. Small quarry at west end of Dalmahoy Hill. In the centre is a cognate xenolith consisting of augite, chlorophæite after fayalite, andesine, and titanomagnetite. The basaltic matrix contains numerous small fayalites, partly replaced by chlorophæite. Ordinary light.  $\times 20$  diameters.

Fig. 3. *Tholeiite of Dalmahoy Type*. Ravelrig Quarry. Coarse-grained variety. The black areas are chlorophæite, sharply separated from the associated intersertal glassy mesostasis. Ordinary light.  $\times 20$  diameters.

Fig. 4. *Dolerite of Dalmahoy Type*. Ravelrig Quarry. The large black patches are all chlorophæite. The mesostasis is crystalline. Ordinary light.  $\times 20$  diameters.

Fig. 5. *Tholeiite of Dalmahoy Type*. Overton, near Kirknewton. A rather coarse-grained variety. Shows the characteristic glassy mesostasis with associated chlorophæite and rods of titanomagnetite. The tendency to euhedrism of the augites is also characteristic. Ordinary light.  $\times 25$  diameters.

Fig. 6. *Basalt of Dalmahoy Type*. Dalmahoy Hill. A cognate xenolith occupies most of the field. The dark areas are chlorophæite replacing fayalite. The clear patches in some of the pseudomorphs are unaltered fayalite. Ordinary light.  $\times 30$  diameters.



Dr ROBERT CAMPBELL and Dr JAMES W. LUNN: "The Tholeiites and Dolerites of the Dalmahoy Syncline."—PLATE I.

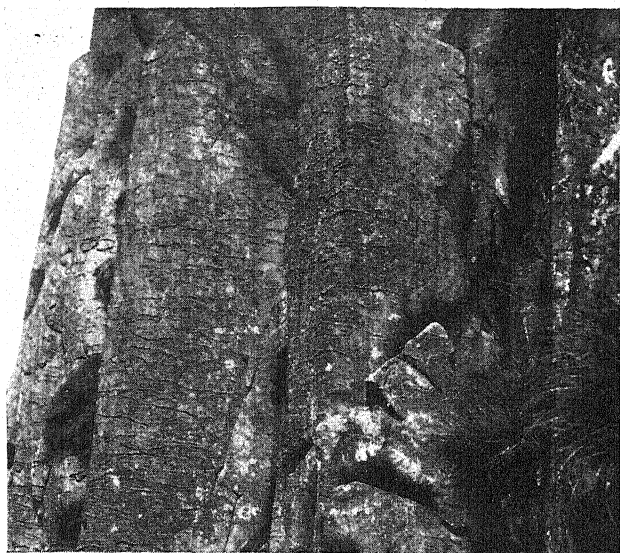


FIG. 1.

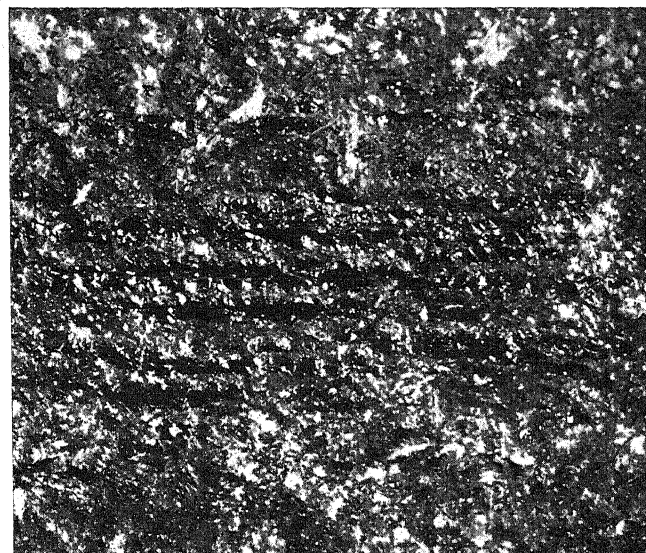


FIG. 2.

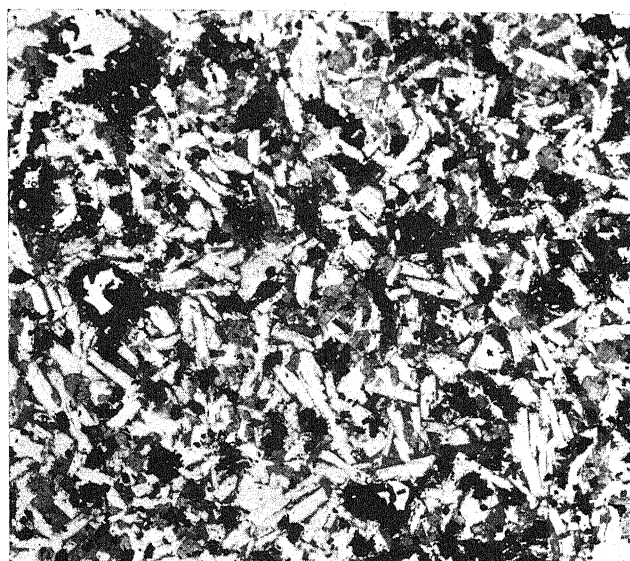


FIG. 3.

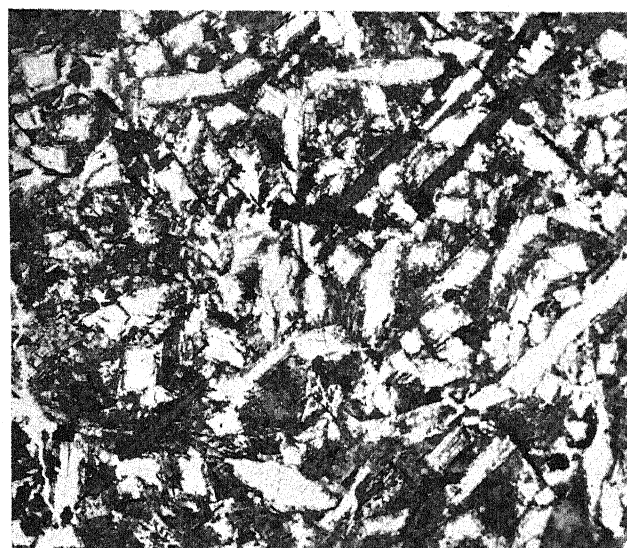


FIG. 4.



FIG. 5.



FIG. 6.





Dr ROBERT CAMPBELL and Dr JAMES W. LUNN: "The Tholeiites and Dolerites of the Dahmahoy Syncline."—PLATE II.



FIG. 1.

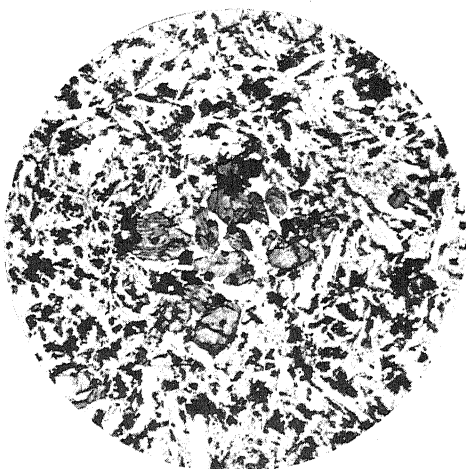


FIG. 2.



FIG. 3.

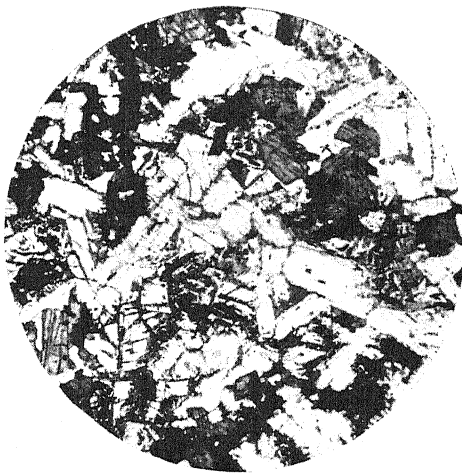


FIG. 4.



FIG. 5.

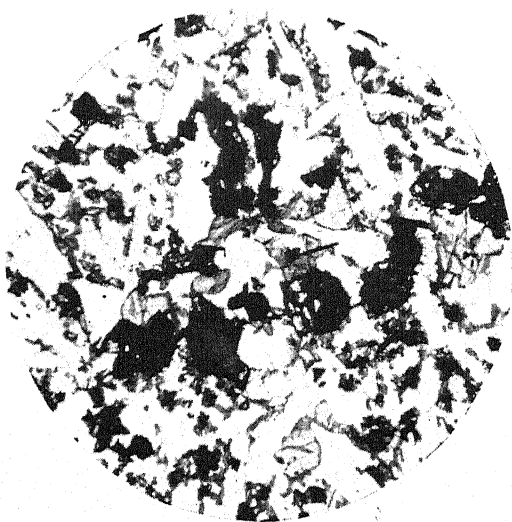


FIG. 6.





XXII.—The Peripheral Innervation of the Uterus.\* By Amy M. Fleming, B.Sc., M.D.,  
Dispensary Surgeon and Pathologist, Royal Samaritan Hospital for Women, Glasgow.  
(From the Physiological Institute, University of Glasgow.) *Communicated by Professor*  
D. NOËL PATON, F.R.S. (With Fifteen Figures in the Text.)

(MS. received March 14, 1927. Read June 6, 1927. Issued separately December 15, 1927.)

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## I. INTRODUCTION.

The present investigation was undertaken to throw some light upon the nature and mode of action of the peripheral nervous mechanism of the uterus.

Previous work has demonstrated that the organ, like other viscera, has an autonomic action. That the uterus and vagina can function independently of the central nervous system has been shown both clinically and experimentally by Sir J. Y. SIMPSON (1), GOLTZ (2), RIEMANN (3), REIN (4), KABIERSCKE and HEIDENHAIN (5), MASIUS (6), and KURDINOWSKY (7).

The nervous mechanism of the uterus may be divided into a central and a peripheral part.

### A. Central Part.

The existence of a centre in the lumbar region was shown by experiments of VALENTIN, BRACHET, LONGET, and BUDGE (9). The fibres destined for the uterus and vagina pass chiefly by way of the splanchnic nerves in the region of the 4th, 5th, and 6th lumbar ganglia (LANGLEY and ANDERSON (8) and (10)). Some preganglionic nerve-fibres form cell-stations in the inferior mesenteric ganglia, others, passing down the aortic plexus into one or other of the two hypogastric nerves, run to more peripheral nerve-cells; occasionally all pass on to these nerve-cells. The hypogastric plexus from which fibres pass to the rectum, internal genital organs, and bladder receives branches from the 3rd and 4th sacral (LANGLEY and ANDERSON (8), (10), and (11)). GASKELL (15) considered that both motor and inhibitory fibres for the musculature of the uterus arise from nerve-cells belonging to the lumbar outflow, there being no evidence that they are connected with the pelvic nerve (LANGLEY and ANDERSON (10), DALE and LAIDLAW (14)).

### B. Peripheral Part.

It is with the peripheral part of the nervous mechanism of the uterus that the present investigation is concerned.

In all viscera this is formed by the emigration of neuroblasts from the embryonic spinal cord, and these remain in synaptic connection with augmentor and inhibitor neurons in the cord. ONODI (48), KUNTZ (49), and ABEL (50).

\* In aid of above research grants were obtained from the Carnegie Trustees and from the Medical Research Council, and are gratefully acknowledged.

(1) *Cervical Plexus or Ganglion*.—The position and relations of the peripheral cell-stations and their morphology are imperfectly known.

LANGLEY and ANDERSON (16) describe in the cat groups of ganglionic cells in the hypogastric nerve near the cervix, and in the rabbit similar cell-stations at the dorso-lateral border of the vagina. From these they find a ganglionated plexus stretching along the vagina. HOLSTE (17) found groups of ganglionic cells in the connective tissue at the level of the cervix in the guinea-pig.

KÖRNER (18) as early as 1863, and POLLE (19) in 1865, are reported by LABHARDT to have discovered in the human subject ganglionic cells in the connective tissue around the upper half of the vagina and the cervix. LEE (21), FRANKENHÄUSER (22), HASHIMOTO (23), and JUNG (24) all described a large cervical ganglion lateral to the uterus in the human subject, whereas PISSEMSKI (25) found ganglia scattered along the branches of the hypogastric plexus at both sides of the cervix. Recently MABUCHI (26) has confirmed this, describing two lateral, two ventral, and a dorsal ganglion at the level of the cervix.

(2) *Intramuscular Nerves*.—According to LABHARDT (20), KILIAN (27) (1851) was the first to demonstrate nerves within the uterine wall of lower animals and man.

FRANKENHÄUSER (22) traced single nerve-fibres to the mucous membrane. GAWRONSKY (28), working on the human subject, the guinea-pig, mouse, sheep, and dog (Golgi's method), described the nerves within the muscle of the uterus as running in thick bundles, dividing into very fine fascicles under the mucous membrane running parallel to its surface and thence sending out vertically into the mucous membrane very fine branches which end in knobs. LABHARDT (20) and MABUCHI (26), however, failed to detect any nerve elements in the mucous membrane of the uterus.

The mode of ending of the nerve-fibres in the muscular coat is still unknown.

KÖSTLIN (29) described minute fibrils ending free or in knobs in the rabbit (Golgi). LABHARDT (20) in man found the nerve-fibrils in the muscle sheath to end sharply, while MABUCHI (26) described small spindle-shaped endings. All three agree that the nerve-fibrils are not sufficiently numerous to allow each muscle-cell to be supplied by one nerve-fibril.

Opinion is divided on the question of the existence of nerve-cells on the nerves within the uterine wall.

According to MABUCHI (26) other workers such as POLLE (19), HENLE (30), LÜSCHKA (31), HASHIMOTO (23), JUNG (24), KRAUSE (32), and J. OGATA (33) describe nerve-cells only outside the uterine wall. KÖRNER (18), MEZINCESCU (34), RÖHRIG (35), REIN (4), and DAHL (36) failed to find ganglionic cells within the wall, although DAHL reports that OUDENAL (37) found small ones in the uterus. On the other hand, GAWRONSKY (28) described cells in the uterine parenchyma such as had been found by PATENKO (38), SCHENK (39), and HERFF (40), and considered them to be nerve-cells. In the case of the cells resembling nerve-cells found by CLIVIO (41), KÖSTLIN (29), HOOGKAMER (42), SPIEGELBERG (43), SPAMPANI (44), and MABUCHI (26) within the uterine muscle, their nature was not proved, as their connection with nerve fibres was not made clear. KEIFFER (45) (Cajal's method) reports the presence of small ganglionic cells within the uterine wall of the cat and guinea-pig. S. OGATA (46) failed in the rabbit to find the ganglionic cells described by BRILL (47) (Cajal's method).

The physiology of the peripheral ganglia of other organs is important.

Much work has been done upon the physiology of the great myenteric plexus in the walls of the alimentary canal (BAYLISS and STARLING (51), MAGNUS (52), CANNON (53)), and its importance in the autonomic control of the movements of the digestive canal is recognised. It is something more than a mere cell-station on the efferent visceral nerves.

The plexuses in the heart wall are generally regarded as mere cell-stations on the inhibitory fibres of the vagus. But the results obtained by LETTERS (54) in this laboratory strongly suggest that they too, at least in the frog, have an autonomic action in controlling the rate of the heart.

The work of SOKOWIN (55) on the influence of the inferior mesenteric ganglia on contractions of the bladder suggests that a peripheral reflex mechanism may exist there, and the possibility of a true reflex existing cannot be ignored, even although the work of LANGLEY and ANDERSON (16) (1894) has led to the conclusion that this is probably an antedromal effect.

The work of MELTZER and AUER (56), and GITHENS (57) on the iris in the cat and rabbit points to the superior cervical ganglion being more than a mere cell-station. The presence of a marked dilata-

tion with adrenaline only after denervation, ANDERSON (58) and ELLIOTT (59) attribute to an increase of excitability of the contractile tissue. POLLOCK (60), working in this laboratory, found that the mydriasis produced by hypophysin was increased by decentralisation and still more by deganglionation of the dilator pupillæ.

Little is known about the function of the peripheral nervous mechanism of the uterus.

KÖSTLIN (29), LABHARDT (20), and MABUCHI (26) agree that sufficient nerve-fibrils do not exist to allow each muscle-cell to be supplied by one nerve-fibre. They conclude that stimulation must pass directly from muscle-cell to muscle-cell as in the ureter (ENGELMANN (64)). More recently KNAUS and CLARK (129), by pharmacological methods, have brought evidence to show that the wave of contraction is conducted partly or entirely through the muscle-cells in the rat's uterus.

The terminal neurons may be of the nature of the common efferent path of the outgoing neurons to skeletal muscle (fig. 1, A), functioning differently according to the nature of the

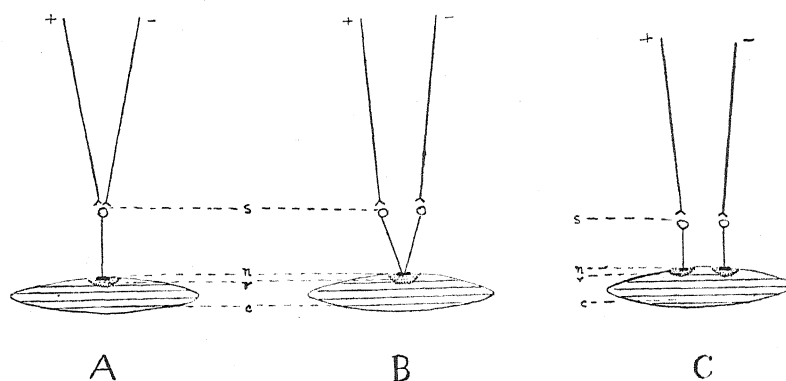


FIG. 1.—To show the three possible forms of the terminal neurones. A, the common efferent path; B, separate augmentor (+) and inhibitor (−) efferent paths acting upon a common receptor substance, *r*; and C, separate augmentor (+) and inhibitor (−) paths, each acting upon a special receptor substance. *s*, cell station; *n*, nerve-ending; *r*, receptor substance; *c*, contractile substance; +, augmentor; and −, inhibitor nerve-fibres in the hypogastric nerve.

impulse reaching them, or they may be of two kinds, one augmentor and one inhibitory, each having independent endings in the muscle-fibres either acting upon a common receptor substance (fig. 1, B) or each provided with a special receptor substance (fig. 1, C) between the nerve-ending and the contractile substance.

It has been very generally accepted that on the course of the visceral fibres there is only one synaptic interruption or cell-station. The evidence for this is by no means conclusive, and in one of his most recent papers LANGLEY (65) admitted that more than one cell-station may exist on the nerves of the intestine. Thus there may be a cell-station in the inferior mesenteric ganglion and another in the cervical ganglion or intramuscular ganglionic structures, if such exist.

## II. PRESENT INVESTIGATION.

The present work is an investigation of the function of the peripheral nervous mechanism of the uterus by the use of anatomical, physiological, and pharmacological methods.

### A. Anatomical Investigation.

While LANGLEY and ANDERSON (16) gave a detailed description of the nerves of the pelvis of the cat and the rabbit, so far the arrangement of these in the rat, guinea-pig, and mouse have not been investigated.



In figs. 2 and 3 the course of the inferior mesenteric plexus and the hypogastric nerves is shown in the rat and guinea-pig.

The hypogastric nerves pass distally in close relationship to the ureter and then towards the uterine wall along with the uterine artery.

In fig. 4 is shown a dissection of the branches of the hypogastric plexus of the guinea-pig and its connections with the 2nd and 3rd sacral nerves. Histological examination confirmed the fact that these strands contain nerve-fibres.

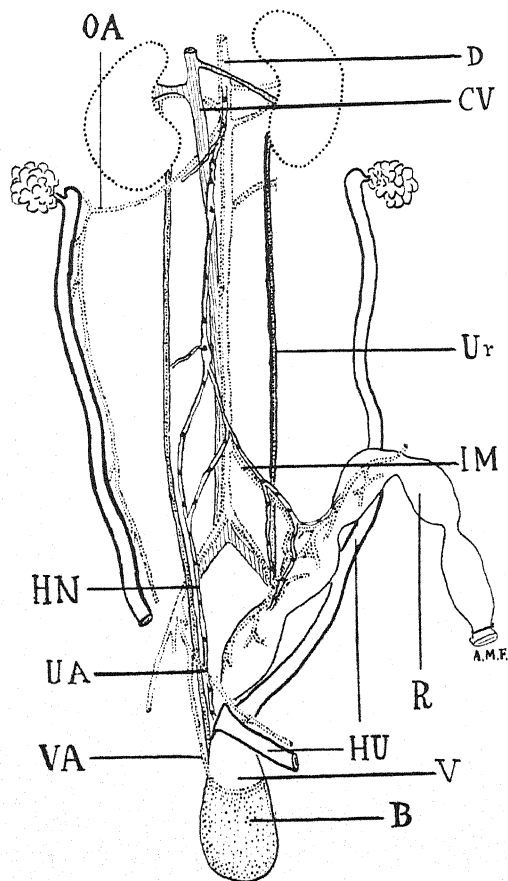


FIG. 2.—Dissection of aortic, inferior mesenteric nerve plexuses, and hypogastric nerves, HN, in the rat. B, bladder; D, descending aorta; CV, inferior vena cava; HU, uterine horn; IM, inferior mesenteric artery; OA, ovarian artery; R, intestine; UA, uterine artery; Ur, ureter; V, vagina; VA, vesical artery.

Complete serial sections of the genital tract of the rat, guinea-pig, and mouse were prepared to locate the positions of the peripheral ganglionic cells in or near the uterus. The vertebral column and pelvic bones were dissected out, and the pelvic contents embedded in paraffin. In the rat serial longitudinal, and in guinea-pig and mouse serial transverse, sections were then prepared, each 10 microns thick.

A few sections were in each series stained with haematoxylin and eosin, and the remainder were prepared by a modification of the methyl-green-pyronin method used by HYRNTSCHAK (66). With this special stain the best results were obtained when the staining in methyl-green-pyronin was continued between two and three hours at 37° C. No better results were obtained by increasing the proportion of pyronin from 0.3 per cent. to 0.6 per cent. The sections were very rapidly dehydrated, and cleared in acetone, absolute alcohol, and xylol. This stain gives the protoplasm of nerve-cells a very bright red granular appearance, which is conspicuous beside the faintly stained wall of the uterus. Each cell contains a light blue nucleus with a red-violet nucleolus.

Nerve-fibres stain less deeply than do the smooth muscle-fibres of the uterus, bladder, and rectum, and the cells forming the coats of the

capillary vessels. Bundles of nerve-fibres in cross-section appear almost unstained and of a glistening appearance.

For each animal a reconstruction has been made with the aid of the glass-plate method, giving the distribution of the branches of the hypogastric nerves and showing the position of groups of nerve-cells on their course. A brief report of each is of interest here.

#### (1) Rat.

*The Cervical Ganglion.*—In a new-born rat ganglionic tissue had been demonstrated by WATSON in this laboratory on each side in close contact with the muscle of the lower part of the cervix (fig. 5).

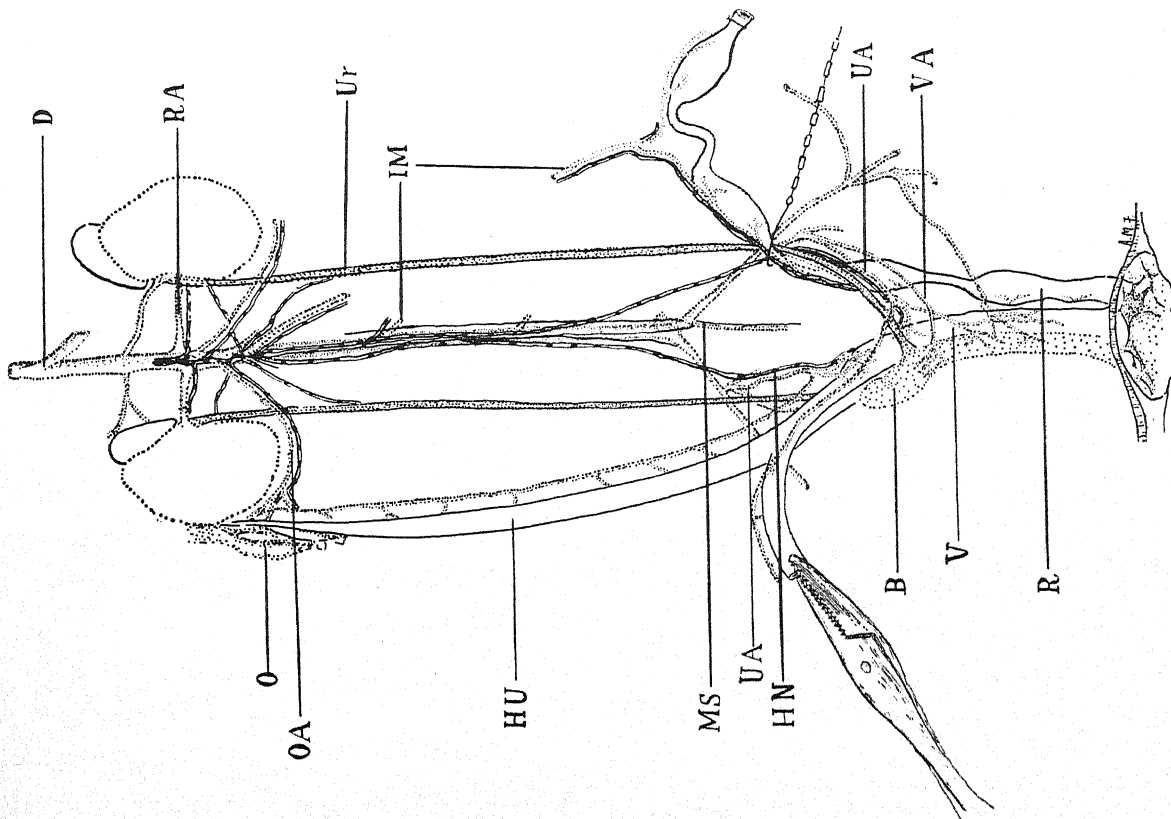


FIG. 3.—Dissection of aortic, inferior mesenteric nerve plexuses, and hypogastric nerves, HN, in the guinea-pig. B, bladder; D, descending aorta; HU, uterine horn; IM, inferior mesenteric nerve; MS, middle sacral artery; O, ovary; OA, ovarian artery; R, rectum; RA, renal artery; UA, uterine artery; Ur, ureter; V, vagina; VA, vesical artery.

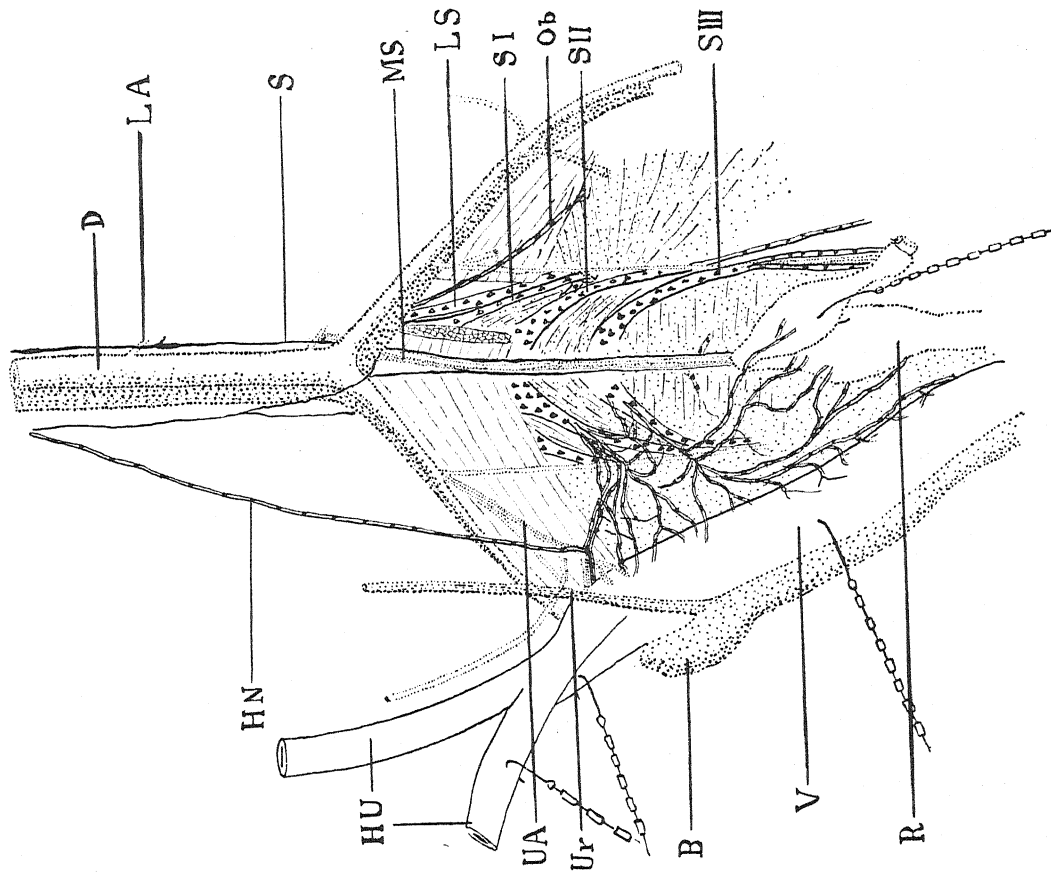


FIG. 4.—Dissection of hypogastric plexus in the guinea-pig. B, bladder; D, descending aorta; HN, hypogastric nerve; HU, uterine horn; LA, lumbar artery; LS, lumbo-sacral nerve trunk; MS, middle sacral artery; Ob, obturator nerve; R, rectum; S, vertebral sympathetic nerve trunk; SI, SII, and SIII, first, second, and third sacral nerves; UA, uterine artery; Ur, ureter; V, vagina.

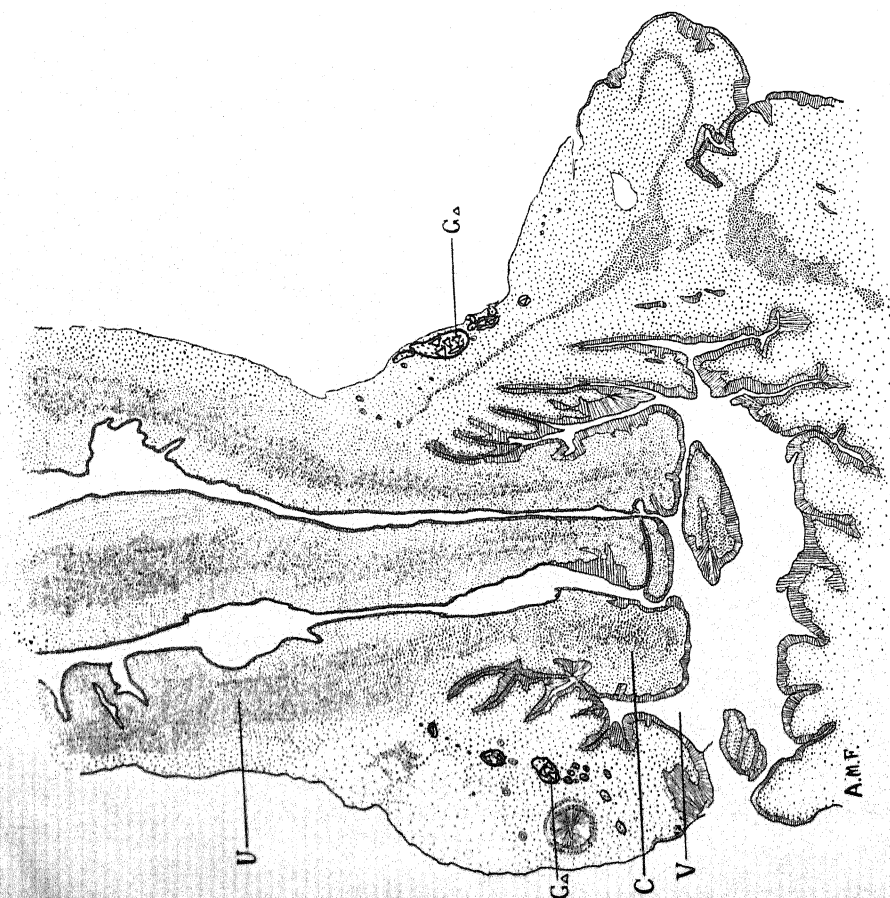


FIG. 5.—Diagram of part of longitudinal section No. 64 of the genital organs of a newborn rat to show the position, GΔ, of nerve-cells in relation to the cervix, C; uterus, U; and vagina, V.

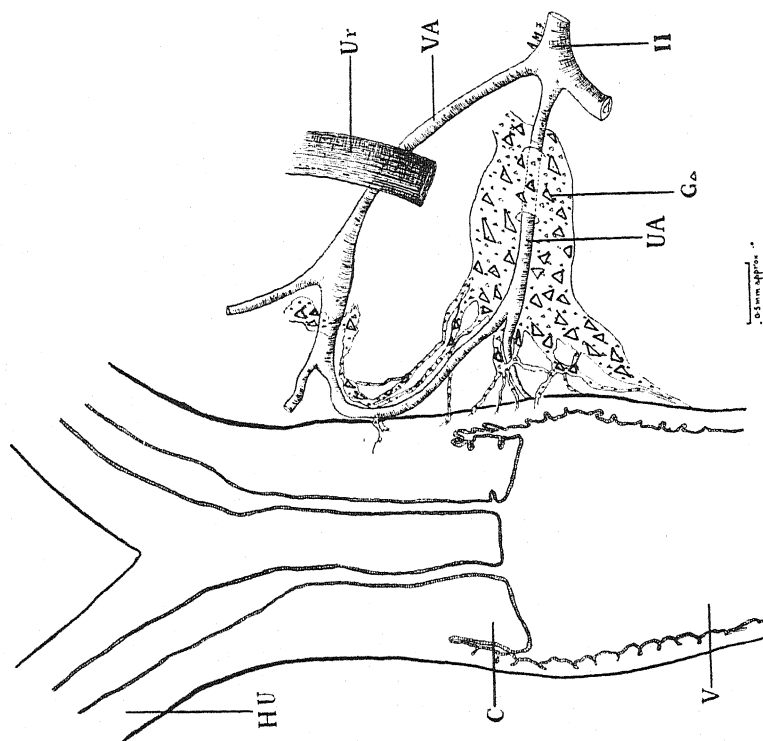


FIG. 6.—Diagram from the reconstruction (posterior view) of the pelvic organs in the adult rat showing C, cervix; GΔ, position of nerve-cells; HU, uterine horn; II, internal iliac artery; UA, uterine artery; Ur, ureter; V, vagina; and VA, vesical artery.



The reconstruction (fig. 6) shows that in the adult rat a large cervical ganglion is present surrounding one of the main branches of the uterine artery, and lying within 0.2 mm. (in this rat) from the lateral wall of the cervix. Besides this large ganglion, scattered groups of cells occur on those portions of the branches of the hypogastric plexus opposite the vagina and the part of the uterus distal to the separation of the two horns.

*Intramuscular Nerve-Cells.*—Portions of uterine wall were stained by the intravital methylene-blue method, but no nerve-cells were found. No cells having the typical stain and morphology of the nerve-cells in the cervical ganglion were found within the uterine muscle, although haematoxylin and eosin, the methyl-green-pyronin, and several modifica-

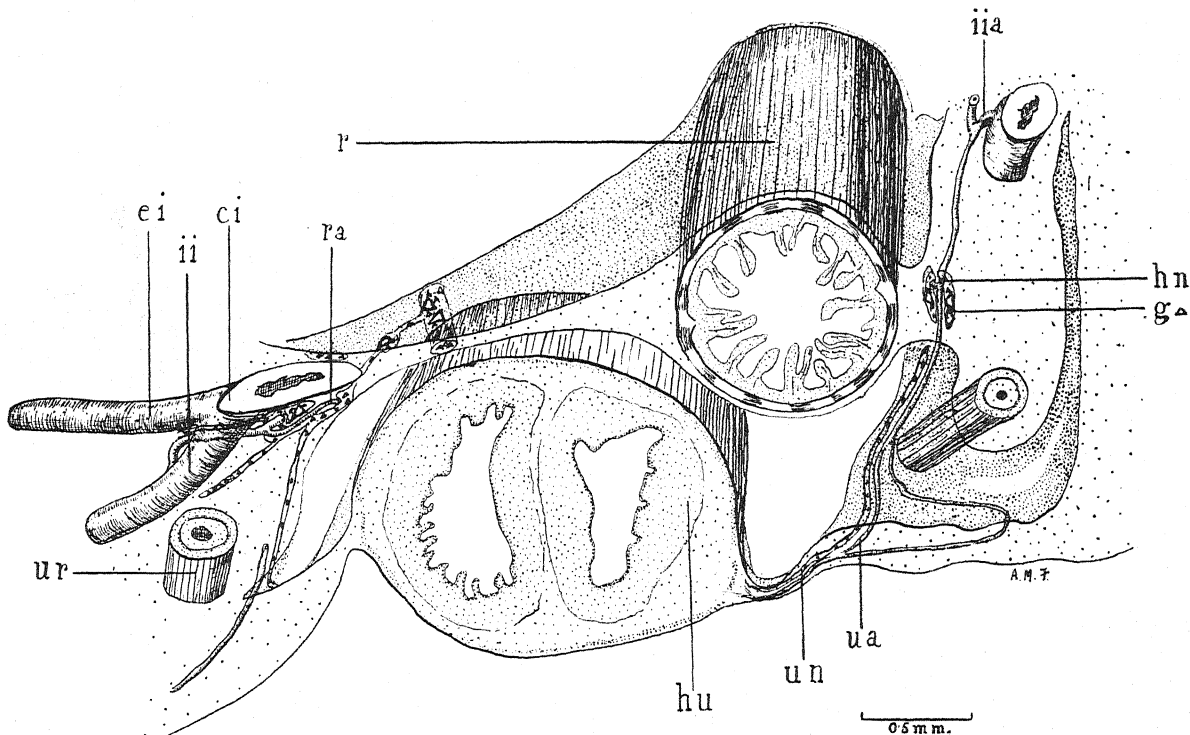


FIG. 7.—Foetal guinea-pig (60 days). Diagram of reconstruction (sections 1449-1595) as seen from the cranial aspect. Showing ci, common iliac artery; ei, external iliac artery;  $g\Delta$ , position of nerve-cells; hn, hypogastric nerve; hu, uterine horn; ii, internal iliac artery; iia, anterior division internal iliac artery; r, rectum; ra, artery to rectum; ua, uterine artery; un, uterine nerve; and ur, ureter.

tions of Nissl staining were employed. In each case the staining was controlled by simultaneous staining of sections of the intestine of the rat. In these control sections nerve-cells were clearly shown in the intestinal wall.

## (2) Guinea-pig.

*Cervical Ganglion.*—Attempts were made to locate the position of the peripheral nerve-cells on the branches of the hypogastric plexus outside the uterine wall in the adult guinea-pig. It was found impracticable to prepare serial sections of a block large enough to include the relatively large uterus and sufficient width of the broad ligament to include the cervical ganglion. For the reconstructions (figs. 7, 8, 9, and 10), therefore, a female foetal guinea-pig of about 60 days' development was used. The 2410 transverse sections are numbered from the vagina proximally.

On the hypogastric nerve ganglionic cells are scattered, but are most numerous on that

part distal to the level of the junction of the horns. From this latter part arise the ganglionated branches supplying the uterus, rectum, and bladder. As in the rat, no ganglionic cells were found on those parts of their course opposite that part of the uterus proximal to the level of the junction of the horns.

The cervical ganglion is less circumscribed than in the rat, and lies close to the uterine artery lateral to the wall of the cervix at this stage of development. As the course of the nerves and arteries cannot be recorded from a glass-plate reconstruction, without to some

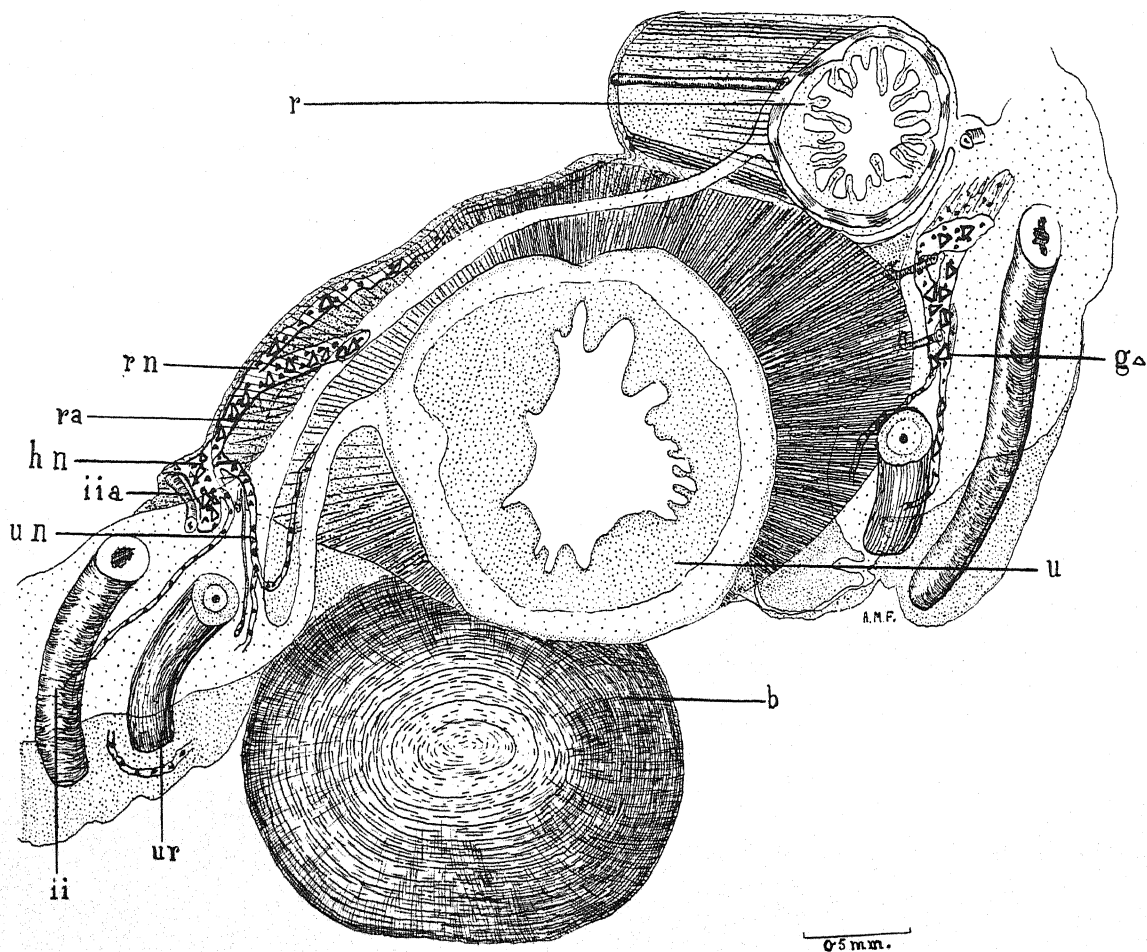


FIG. 8.—Foetal guinea-pig (60 days). Diagram of reconstruction (sections 1252-1449) as seen from the cranial aspect. Showing *b*, bladder, *gΔ* position of nerve-cells; *hn*, hypogastric nerve; *ii*, internal iliac artery; *iia*, anterior division internal iliac artery; *r*, rectum; *ra*, artery to rectum; *rn*, nerve to rectum; *u*, uterus; *un*, uterine nerve; and *ur*, ureter.

extent projecting them on to the topmost of the series of sections, a graphical reconstruction (fig. 10) was also made. Fig. 10 shows the nerves and arteries passing to the uterus, cervix, and vagina. As in the other drawings, the nerve tissue is indicated by very coarse stippling, and the positions of nerve-cells are indicated by the presence of a small triangle. This diagram demonstrates the widening out of the uterus indicated by the radial shading in fig. 8.

*Intramuscular Nerve-Cells and Fibres.*—In the above series of sections, in which the nerve-cells within the wall of the intestine and bladder were clearly shown up, with the methyl-green-pyronin staining, there were no similar cells seen within the uterine wall. The contrast is very visible because on each slide a section is seen of the entire pelvic contents. No typical nerve-cells were found in three series of longitudinal sections of the uterus of new-born

guinea-pigs stained by haematoxylin and eosin, by Nissl's staining, and by Cajal's method respectively.

Portions of the uterus and of the small intestine of the guinea-pig were stained simultaneously by Cajal's, and others by Bielschowsky's method. Nerve-cells and non-medullated nerve-fibres were identified in the intestinal wall, but although non-medullated nerve-fibres were seen in the uterine wall, no typical nerve-cells have so far been found.

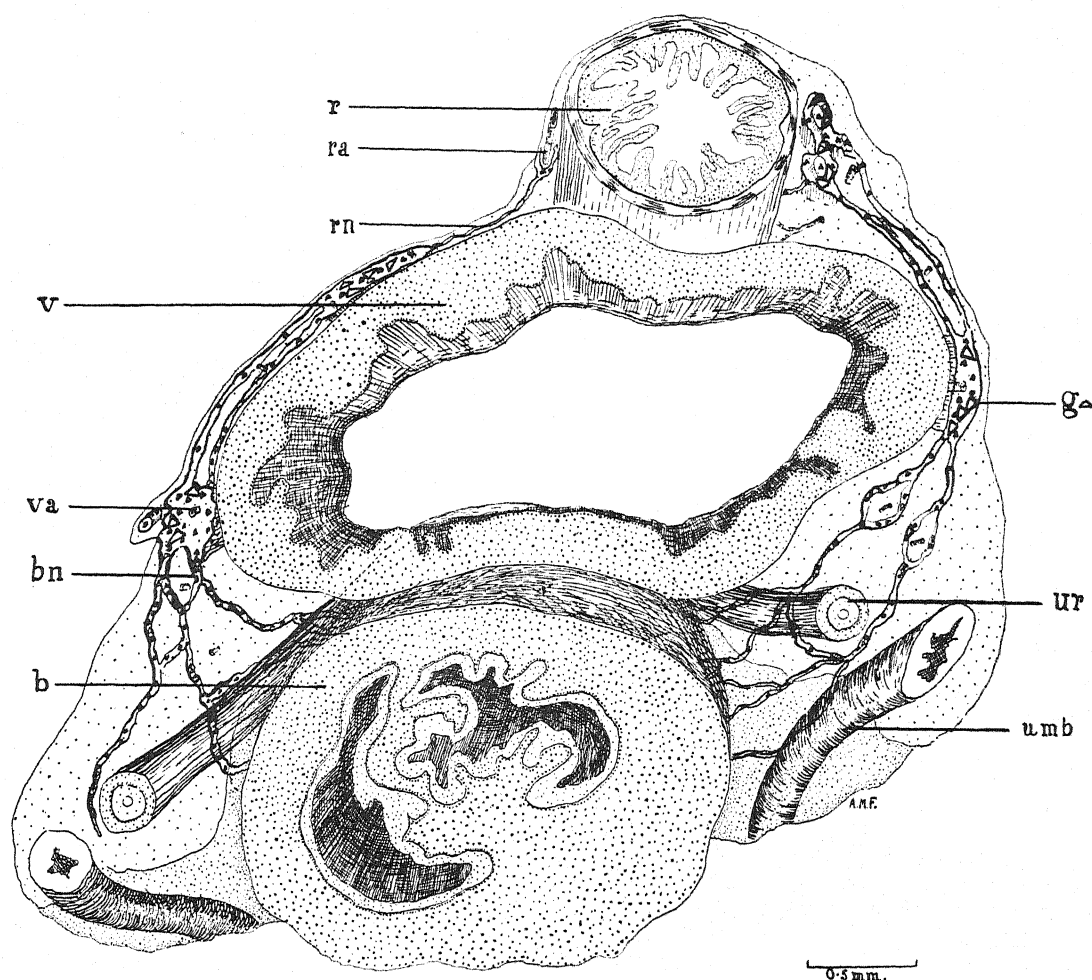


FIG. 9.—Foetal guinea-pig (60 days). Diagram of reconstruction (sections 1032-1252) as seen from the cranial aspect. Showing *b*, bladder; *bn*, nerve to bladder; *gΔ*, position of nerve-cells; *r*, rectum; *ra*, artery to rectum; *rn*, nerve to rectum; *umb*, umbilical artery; *ur*, ureter; *v*, vagina; and *va*, vaginal artery.

### (3) Mouse.

No dissections of the hypogastric nerves were made in the mouse, because in a mouse about one week old the sympathetic nerves to the uterus could be traced in transverse sections from the inferior mesenteric ganglia. In this series the 684 sections are numbered from the vaginal end proximally. From the aortic plexus, lying first anterior to the inferior vena cava and then anterior to the aorta, a ganglionated nerve plexus passes to the intestine along with the tortuous inferior mesenteric artery. Just distal to the bifurcation of the aorta the aortic plexus divides into the hypogastric nerves, which pass downwards and forwards on either side of the rectum. The hypogastric nerve begins to divide to form the hypogastric plexus



1 cm. below the level at which the horns unite, *i.e.* at the same level at which the cavities of the horn fuse to form one. These branches have nerve-cells on their course, but these are restricted to those parts distal to a level about 0.5 cm. below the fusion of the cavities of the horns. The nerve-cells are especially numerous lateral to the vaginal fornix. Here the plexus intertwines with the vaginal branches of the uterine artery, and sends divisions anterior and posterior to the vaginal fornix (fig. 11). The anterior ganglionated strand passes mainly

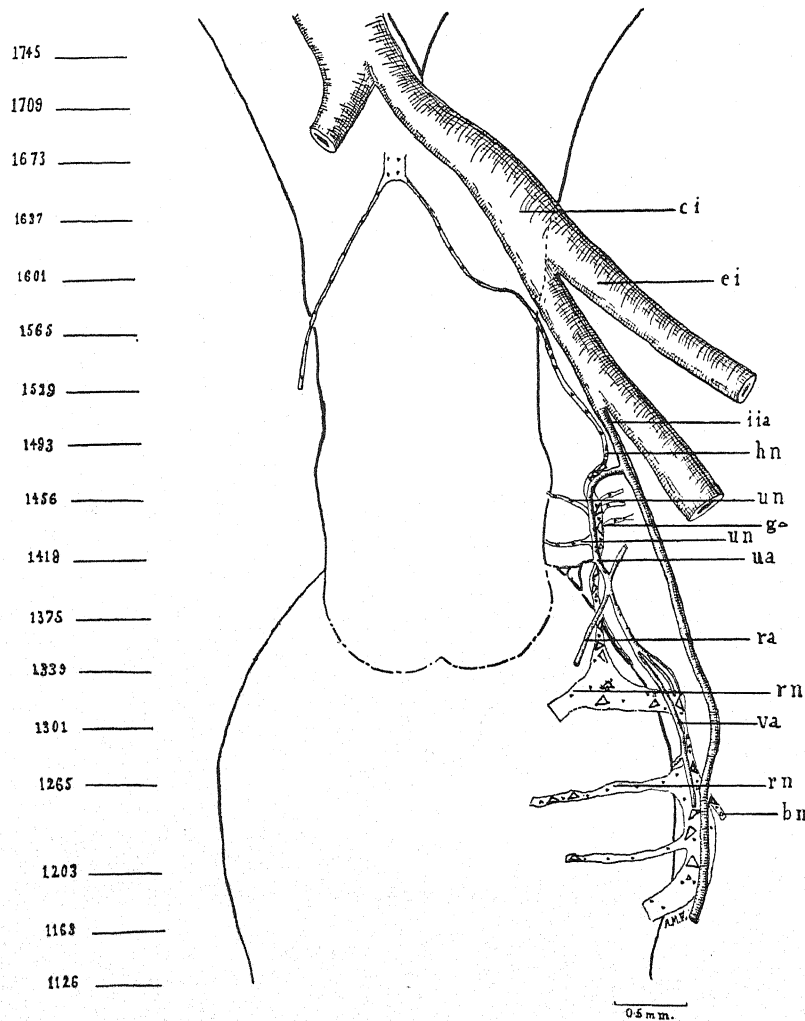


FIG. 10.—Fœtal guinea-pig (60 days). Graphical reconstruction of the nerves and arteries to the uterus and vagina (sections 1126–1745). *bn*, nerve to bladder; *ci*, common iliac artery; *ei*, external iliac artery; *hn*, hypogastric nerve; *ia*, anterior division internal iliac artery; *ga*, position of nerve-cells; *ra*, artery to rectum; *rn*, nerve to rectum; *ua*, uterine artery; *un*, uterine nerve; and *va*, vaginal artery.

to the bladder, but ganglionated branches also pass to the adjacent vaginal wall. On the branches of the anterior division ganglionic cells cease to be numerous distal to the upper end of the urethra.

The posterior ganglionated division gives off branches accompanying the arteries running down the postero-lateral surface of the vagina. A distinct cervical ganglion is not seen in the mouse; instead there is a ganglionated plexus lying within .02 cm. of the vaginal fornix.

**Intramuscular Nerve-Cells.**—Sections of intestine and of bladder treated along with the uterus showed the presence of nerve-cells staining characteristically with either methyl-green-pyronin or Nissl's staining, yet no definite and distinct nerve-cells were seen in the

uterine wall, nor in portions of the horn of a pregnant mouse almost full-time stained by various modifications of Cajal's method, including that of Ranson, and also by Donaggio's method.

Bodies somewhat resembling nerve-cells were found in the uterine wall of these three animals. These cells showed greater affinity for the silver staining than did the surrounding connective tissue and muscle. Some of these cells had an irregular outline occasionally

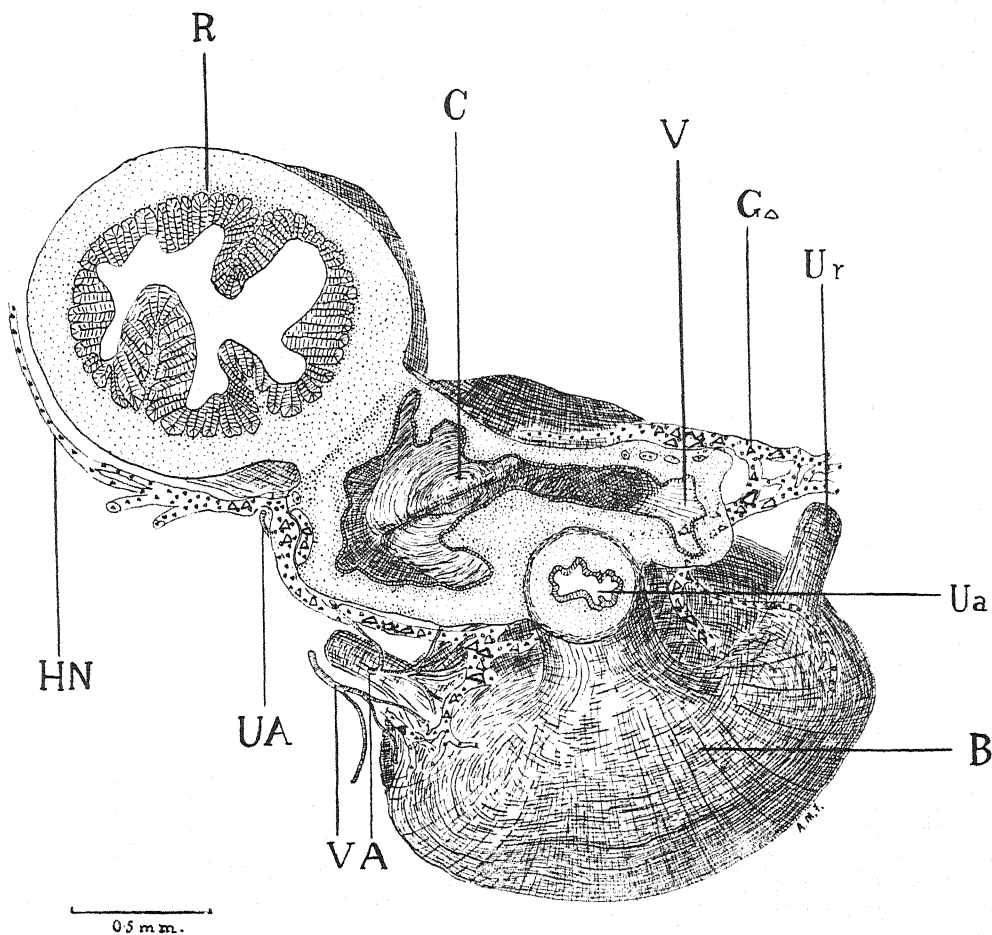


FIG. 11.—Mouse. Diagram of reconstruction (sections 647-785) seen from caudal aspect. Showing B, bladder; C, cervix;  $G\Delta$ , position of nerve-cells; HN, hypogastric nerve; R, rectum; UA, uterine artery; Ua, urethra; Ur, ureter; V, vagina; and VA, vesical artery.

sufficiently marked to resemble blunt processes, and in some instances in addition to these processes a fibre of some length and impregnating with silver was seen. But the fact that they do not stain with either methyl-green-pyronin or Nissl's staining while other ganglionic cells do, makes it improbable that they are nerve cells.

### B. *Physiological Investigation.*

The problem is to determine the part played in the autonomic control by the cervical ganglion.

In the first place, an attempt was made to study whether there is any difference in the action of the excised uterus with and without the ganglion. The conclusion is warranted that the ganglion cells continue to act in such preparations.

*Method.*—A series of experiments were carried out on the isolated uterus of the guinea-pig and of the rat, using a modification of the apparatus of MAGNUS (52) and of DALE and LAIDLAW (67).

One glass tube, on the closed lower end of which three small hooks had been fused, and having a perforation above the hooks, was used as an inlet for oxygen and to anchor the muscle strips. The formula of the Tyrode was NaCl 0.8 per cent.; KCl 0.02 per cent.;  $\text{CaCl}_2$  0.02 per cent. (crystals).  $\text{NaHCO}_3$  0.1 per cent.;  $\text{MgCl}_2$  0.01 per cent.;  $\text{NaH}_2\text{PO}_4$  0.005 per cent.; glucose 0.1 per cent.; the  $\text{NaHCO}_3$  being dissolved before the addition of the  $\text{CaCl}_2$ .

In each case the  $p_{\text{H}}$  was lowered to 7.4, as at this the uterus of both the rat and the guinea-pig contracted well.

The Tyrode was changed by syphon action without the tissues being exposed. It was introduced from a height through a funnel, through as short a length of rubber tubing as possible, then through a glass tube, the cavity of which was continuous with that of the lower end of the bath. A tube passed from the upper part of the cavity of the bath and acted as an overflow exit. The capacity of the bath was 30 c.c. The bath was surrounded by a water-bath, the temperature being regulated by heating a projecting limb attached to it. The rubber tubing and funnel were kept when not in use in a large water-bath at  $37.5^\circ\text{C}$ . The apparatus was only sufficiently accurate to maintain the temperature of the bath between  $36.5^\circ$  and  $37.5^\circ\text{C}$ .

It was found necessary to keep the rate of inflow of oxygen into the bath uniform, since if the rate suddenly increased both the tone and the amplitude of the contractions decreased. LOVATT and UNDERHILL (73) found that the tone of plain muscle varies with the rate of introduction even of an indifferent gas.

When the Tyrode solution remained in contact with the uterine strips and exposed to the air and to the stream of oxygen, its hydrogen-ion concentration was found to change. In two experiments the  $p_{\text{H}}$  had increased from 7.5 to 7.8 during intervals of 100 and 110 minutes. The contractions decreased in amplitude the longer the strips remained in the same Tyrode. No attempt was made to determine whether this was in part due to the development of some derivative such as LE HEUX (74), ARAI (75) and MAGNUS (76) described in the intestine, and ENGELHARD (77)—according to MAGNUS—and BACHMAN (78) in the uterus, but, to eliminate error arising from this change, the solutions in the bath were changed frequently.

*Material Used.*—The experiments were made on the isolated uterus of the rat and guinea-pig. The rats weighed 104–230 grm. and the guinea-pigs 370–600 grm. The uterus of the mouse was too small for this work. The uterus of the rat was preferable for two reasons, viz. (1) because of the absence of the large spontaneous variations of tone which are a feature of the isolated guinea-pig's uterus contracting in Tyrode  $p_{\text{H}}=7.4$ ; (2) because of the proximity of the cervical ganglion to the uterine wall.

As in each experiment the strips being compared were taken from the same animal, it was considered unnecessary to identify the stage in the oestrus cycle which the work of BLAIR (79), KEYE (126), and SECKINGER (127) have shown to modify the character and the rate of conduction (KNAUS and PARKES (128)) of the contractions.

*Preparation of the Strips.*—The animal was killed by a blow on the head and by cutting its throat. In some cases it was given a small initial dose of ether. To facilitate the removal of the broad ligament intact the anterior wall of the pelvis was removed. The ovaries, uterus, and vagina were excised without the muscular part being touched with instruments, and were placed at once in Tyrode kept at about  $37^\circ\text{C}$ . The strips were treated identically, the risk



of injury being reduced by using a very fine needle and silk. The ovaries were detached from the strips before they were placed in position in the bath. The strips to be compared differed in that one was free and one attached to the cervix, carrying with it the broad ligament including the cervical ganglion. They are named for convenience the "non-ganglionated" and "ganglionated" strips respectively. A comparison was made between corresponding parts of opposite horns, uterine and ovarian ends of the same side and of opposite sides, and between the ovarian end and a strip including the uterine end of the horn and the cervix. The measurement of the strips was made after they had been overnight in cold Tyrode without oxygen.

### RESULTS.

#### 1. Behaviour of either Horn of the Uterus: (a) one with, (b) one without the Ganglion.

The contractions in certain rats gave tracings of pendulum-like regularity. In others smaller contractions were superadded to the simple waves. The occurrence of these small superadded contractions differed irregularly from one animal to another. Their number might alter and they might show themselves anywhere on the curve. Neither their number nor their position was determined by the presence or absence of the attachment of the cervical ganglion.

Especially at the beginning of the experiments, variations occurred in the state of tonus upon which the contractions were superadded. The two strips differed in most experiments in irregularity, but although in 75 per cent. it was greater in the ganglionated strip, the number of exceptions prevented this from being attributed to the influence of the cervical ganglion. Some, but not all, of the experiments showed differences between the two strips in the rapidity with which the relaxation followed the contraction and the rate at which the contraction passed off, but there was no difference between the non-ganglionated or ganglionated strip. The rate of contraction was greater in the non-ganglionated strip in 13 per cent., in the ganglionated in 56 per cent., and was equal in both in 31 per cent.

A comparison between the rates of contraction of strips taken from opposite ends of a horn—both strips being unattached to the ganglion—showed that in three out of four experiments the rate of contraction of the strip from the ovarian end was greater than that from the vaginal end (fig. 12).<sup>\*</sup> This greater rate of the strip from the ovarian end was not determined by its length relative to that from the vaginal end, as its rate was more rapid both when it was the longer and when the shorter (fig. 12). In the remaining experiment,

<sup>\*</sup> The tracings read left to right, the upstroke representing contraction and the downstroke relaxation. A centimetre scale has been marked on each tracing before reproduction.

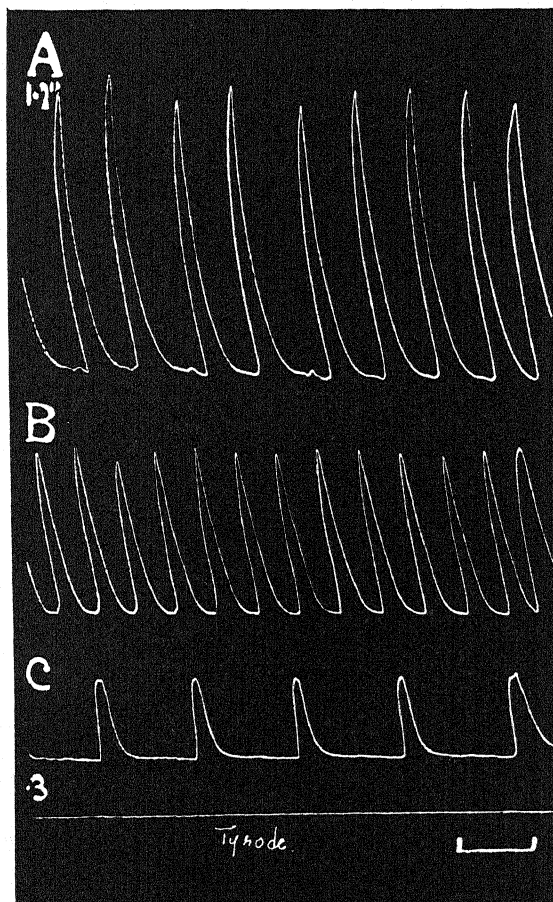


FIG. 12.—Uterus, non-pregnant rat. Comparison between contractions of A, whole horn, 1.2 inches; B, ovarian end, 0.75 inch; C, vaginal end of the horn, 0.3 inch.

on account of there being smaller contractions superadded to the main contractions, the rate of the strip from the ovarian end was too irregular for a comparison to be made. These results confirm those of KEHRER (80), who showed that in the cat, dog, and rabbit each part of the uterus shows a different type of contraction, and of OGATA, S. (46), who found that the ovarian end contracted more rapidly than the remainder of the isolated horn of the non-pregnant rabbit.

One of the factors, therefore, determining the variations in the relative rate of the two strips is their position in the horn, and the strips rarely correspond exactly because during their preparation the horns vary continually in their state of contraction.

(2) *Behaviour of a Horn of the Uterus: (a) before, (b) after removal of the Ganglion.*

A comparison was made between the tracings before and after removal of the ganglion in the following experiments. In each the trauma to the two strips was equalised by a small piece being cut off beyond the end of the non-ganglionated strip. Any change in the base line of the tracing before and after the operation depended not only on a change in the tone of the strips and on the depth to which the strips were sunk in the bath, but also on the approximation of the levers to the drum. Although, therefore, a very slight modification of the tone, if equally marked in the two, might escape being registered, a difference between the two in any change of tone produced would be demonstrated.

#### EXPERIMENTS.

1. Both strips were taken from the ovarian end of the horn. The longer ganglionated strip contracted the more slowly. After removal of the ganglion there was no difference between the two strips in the degree of any slight change of tone produced. No change in the form of the tracing occurred on removal of the ganglion.

2. Both strips were taken from the ovarian end of the horn and were equal in length. Their contraction rates were almost equal. No change of tone followed removal of the ganglion. A slight decrease in amplitude occurred only in the strip from which the ganglion had been removed. An increase in rate occurred in both strips after the operation, but the change was equally marked in the two strips. The form of the tracing was not modified by removal of the ganglion, although slight temporary arrhythmia occurred, especially in the deganglionated strip.

3. Both strips were taken in this experiment from the ovarian end of the horn. Their length and their rate of contraction were practically equal. There was no difference between the two strips after removal of the ganglion (fig. 13).

The same operation was also performed in four experiments, in which, however, the strips had been treated already by physostigmine 1 : 6200 or by pilocarpine 1 : 5000 or 1 : 2500 since these drugs are not known to poison the ganglion in these strengths. Their previous use lessens the value of the experiments. In none of these was there any marked difference after removal of the ganglion.

#### CONCLUSIONS.

(a) This method of investigation affords no evidence of any direct action of the cervical ganglion on the movements or tone of the excised uterus. This finding agrees with that of KEHRER, who stated that the form of contraction typical of each specific part of the genital

tract in the rabbit, cat, and dog was unaltered by the removal of part of the surrounding pelvic tissues or their complete removal up to the muscle wall.

(b) The point of origin of the impulse initiating and controlling the movements of the uterus therefore appears to lie within the uterine substance itself.

(c) The rate of the contractions occurring at the ovarian end is quicker than at the vaginal end of the horn.

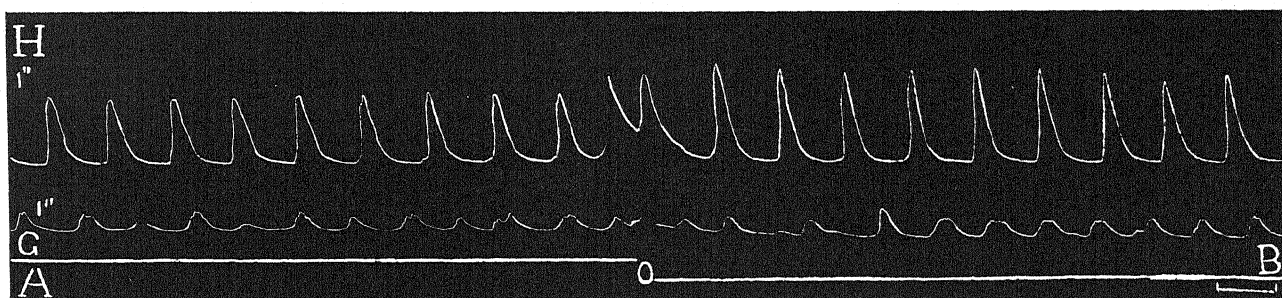


FIG. 13.—Uterus, non-pregnant rat. Comparison between the movements of the non-ganglionated H and the ganglionated G horn before—AO—and after—OB—removal of the cervical ganglion.

### C. Pharmacological Investigation.

It seemed that a study of the action of drugs—known to act upon the peripheral nervous mechanism of viscera—upon the uterus, with and without the cervical ganglion, might throw further light upon its possible action.

For this purpose the following drugs were selected:—

1. Barium, as acting directly on the contractile substance of muscle (*Text-book of Pharmacology*, CUSHNY, p. 569).
2. Adrenaline, as stimulating the endings of the true sympathetic neurons or their receptor substance in muscle (*op. cit.*, p. 372).
3. Pilocarpine, as stimulating the receptor substance (*op. cit.*, p. 342) of the true and the para-sympathetics.
4. Physostigmine or Eserine, a representative of the Muscarin group, as stimulating the neural endings (*op. cit.*, p. 351).
5. Atropine, as blocking nerve action at the level of the receptor substance (*op. cit.*, p. 323).
6. Nicotine, as acting upon the peripheral ganglion-cells, first to stimulate and then to paralyse (*op. cit.*, p. 314).
7. Ergotamine and Ergotoxine, stimulating and then paralyzing the augmentor receptor substance (*op. cit.*, p. 377).

To make such a clear-cut classification is of course unwarranted, since the characteristic action of each substance depends upon the concentration, *i.e.* the dose, and upon the condition of the structures acted upon. Not only may the stimulating action of a moderate dose be converted into a paralyzing action by larger doses, but the mere continuance of the presence of the drug may alter the reaction of the tissues to it. Further, while the primary action may be upon one of the tissues present, *e.g.* upon, say, the receptor substance, greater concentration or prolonged action may result in a spread of the effect to other parts.



In the following description of the action of these drugs the tone and contractions, although not necessarily independent, are dealt with separately. As regards the contractions, their rate and amplitude were measured. The relation of tone and amplitude is somewhat complicated. There may be a concomitant increase of both; on the other hand, a marked increase of the tone may decrease the amplitude of contraction.

(1) *The Action of these Drugs on the isolated Uterus of the Rat and of the Guinea-pig.*

(1) *Barium*.—I found that in all strengths of barium chloride used there was an increase in tone and in the rate of the contractions in the rat's uterus. In weak solution 1 : 75,000–1 : 10,000 there was an increase in their amplitude, whereas stronger solutions produced a decrease in amplitude or the disappearance of contractions.

On the uterus of the guinea-pig a marked augmentor effect was also produced by barium chloride in solutions varying from 1 : 2500–1 : 1670.

This confirms the work of ITAGAKI (83) on the isolated uterus of the rat, of FARDON (82) on the guinea-pig's uterus *in situ*, and of KEHRER (80) on the cat. It is in line with that of OGATA (46) on the rabbit.

(2) *Adrenaline*.—The effect of adrenaline in concentrations varying from 1 : 10,000–1 : 85,000 was tested in eighteen of my experiments, and it was found that both in the pregnant and non-pregnant uterus of the rat there occurred a decrease of the tone and of the rate and amplitude of the contractions. The response to adrenaline in concentrations varying from 1 : 1,000,000–1 : 16,000 was also an inhibitory one in the pregnant and the non-pregnant uterus of the guinea-pig. In ten experiments the uterus was non-pregnant, and in two pregnant.

An inhibitory effect has been found by other investigators on the uterus of the non-pregnant cat (KEHRER (80), HILZ (85), BARGER and DALE (86), DALE (87), CUSHNY (88), QUAGLIARIELLO (89), BACHMAN and LUNDBERG (90), DALE and LAIDLAW (91)); on the dog (KEHRER (80), HILZ (85)); on the guinea-pig (NICULESCU (98), COW (99), ADLER (100), OKAMOTO (94), GUNN and GUNN (101), SUGIMOTO (102), HILZ (85), BACHMAN and LUNDBERG (90)); on the mouse (ADLER and BACHMAN (100)); and on the rat (GUNN and GUNN (101), OKAMOTO (94)). On the other hand, augmentor effects are found in the pregnant cat (KEHRER (80), KURODA (92), OKAMOTO (94), CUSHNY (88), QUAGLIARIELLO (89), BACHMAN and LUNDBERG (90)); occasionally in the pregnant dog (NEU (96), KURODA (92)), and the pregnant guinea-pig (KEHRER (80), QUAGLIARIELLO (89), SUGIMOTO (102)); in the rabbit (KEHRER (80), LANGLEY (84), KURDINOWSKY (7), OKAMOTO (94), GADDUM (105)); in the human subject (KURDINOWSKY (7), KEHRER (80), NEU (96), TUROLT (103), RÜBSAMEN (104)); in the virgin monkey (DALE (87)), and ferret (DALE (97) and BACHMAN and LUNDBERG (78)); and in the non-pregnant cow (MEYER (95)).

(3) *Pilocarpine*.—The response of the isolated uterus of the rat to pilocarpine in concentrations varying from 1 : 10,000–1 : 2000 was studied in six of my experiments. In each experiment two or three strips were compared at once. The effect was found to be inconstant. In four experiments one or other of the strips showed very little response to pilocarpine, only a slight increase in rate being observable. An increase of the tone and of the amplitude and rate of the movements was the most frequent sequel to treatment with pilocarpine. Occasionally a decrease in rate, however, occurred. Strips taken from the ovarian and uterine end of the same horn differed in response, but no variety of response was observed to be characteristic of either end of the horn. In two experiments—both pregnant rats—decrease in tone and in

the rate and amplitude of the contractions occurred, but in each case only in one of the strips under comparison (fig. 14). In one experiment this strip had already given an augmentor response to a weaker solution of pilocarpine, 1:5000. Augmentation was produced in the other strip in this experiment by pilocarpine in the stronger (1:2500) (fig. 14), as well as in the weaker solution (1:5000). In the other pregnant rat no response took place in the other horn, although the solution was fairly concentrated (1:2000).

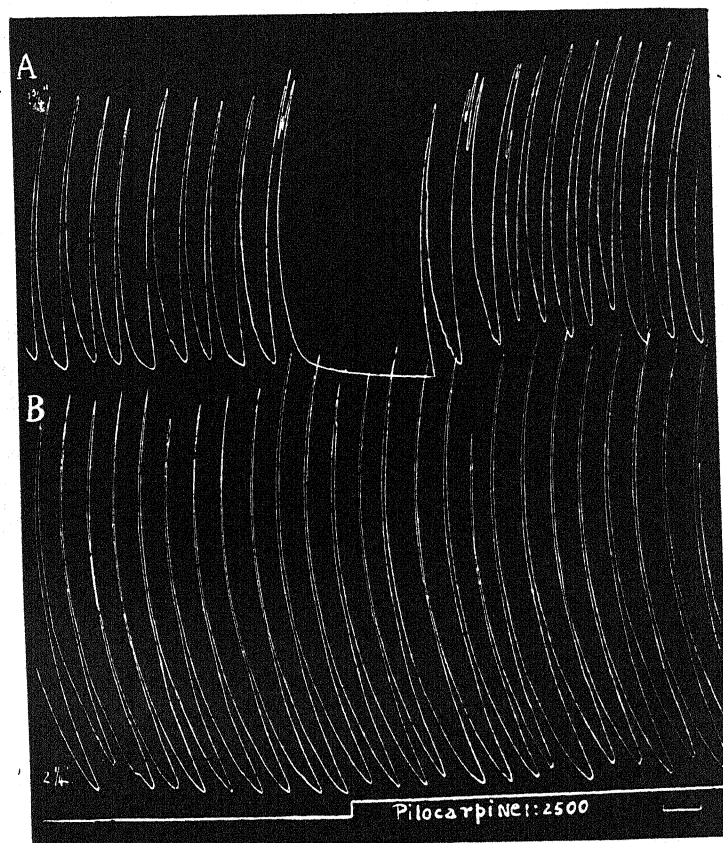


FIG. 14.—Uterus, pregnant rat. Comparing the effect of pilocarpine 1:2500 on the ganglionated (A) and the non-ganglionated (B) horn.

In both the pregnant and the non-pregnant uterus of the guinea-pig a slight augmentor effect was produced by pilocarpine (1:5000–1:2000).

These results confirm those of previous workers, who found that the action of pilocarpine on the uterus is generally augmentory, *e.g.* on the non-pregnant guinea-pig (OKAMOTO (94), DALE and LAIDLAW (14), SUGIMOTO (102)), the rat (OKAMOTO (94), ITAGAKI (83)), the pregnant cat (CUSHNY (88), FARDON (82)), the non-pregnant cat (DALE and LAIDLAW (14), KEHRER (80), OKAMOTO (94)), the rabbit (CUSHNY (106), OKAMOTO (94), OGATA (46)), but may in some cases be inhibitory, *e.g.* in the non-pregnant cat *in situ* (CUSHNY (88)), in the rat, pregnant and non-pregnant (ITAGAKI (83), GUNN and GUNN (101)), while sometimes no effect is obtained, as in the isolated pregnant guinea-pig and the rat (GUNN and GUNN (101)).

The inhibition produced in the uterus of the two pregnant rats by strengths of 1:2000 and 1:2500 is difficult to explain. It was not due to a more prolonged action, as it occurred immediately in each case. In one experiment the uterus had not been treated before with pilocarpine. In the other an augmentory effect had been got before with pilocarpine, 1:5000, and was again got with 1:2500 later in the experiment. This also is against its being due to

greater concentration, as is also the fact that in each experiment it was obtained only in one of the two strips.

(4) *Physostigmine (Eserine)*.—In my investigation the effect of physostigmine (1:795–1:3000) was recorded on the uterus in five rats, one only being pregnant. After weaker solutions very little response was seen in some strips, but the usual effect was an increase in tone and in the rate and amplitude of the movements (fig. 15).

Strengths of 1:775 and of 1:1550 in the case of certain strips produced a decrease of tone and of the rate and amplitude of the contractions.

An augmentor effect was produced in both the non-pregnant and pregnant uterus of the guinea-pig, using the strengths 1:4600–1:800. This is similar to the effect reported on the uterus of the cat by FARDON (82), KEHRER (107), CUSHNY (106), and on that of the bitch and guinea-pig by FARDON (82).

An inhibitory effect following physostigmine has not before been recorded in the literature available to me. These results probably illustrate the fact that while moderate doses stimulate, large doses depress and paralyse.

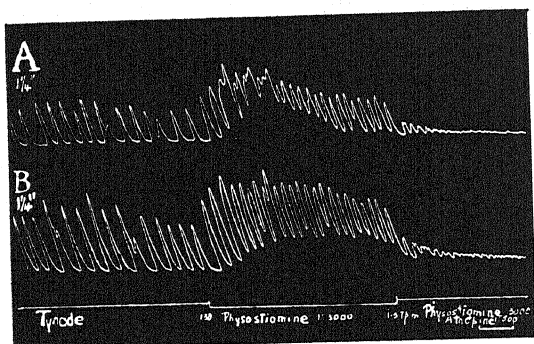


FIG. 15.—Uterus, non-pregnant rat. Comparison between the effect of physostigmine 1:3000, followed by atropine 1:500 upon the non-ganglionated (A) and ganglionated horn (B).

(5) *Atropine*.—In eleven experiments strips from the horn of the rat—two only being pregnant—were submitted to treatment with atropine (1:200–1:2000). With the weaker solutions an increase in tone associated with a decrease in amplitude and an increase in rate occurred. Stronger solutions produced an inhibitory effect, especially if the increase in concentration occurred suddenly. It is to be noted that the strengths used are not the same as those used by ITAGAKI (83).

In the guinea-pig—three being non-pregnant and one pregnant—slight augmentation was recorded on treatment with atropine (1:1000).

The inhibitory effect obtained is probably an example of the depressor effect of any drug in very strong concentration.

Similar augmentor effects have been obtained by other investigators on the uterus of the cat and dog (KEHRER (80)), of the virgin ferret (BACHMAN and LUNDBERG (90)), the guinea-pig (BACHMAN and LUNDBERG (90), SUGIMOTO (102)), the mouse (ADLER (100)), rabbit (OKAMOTO (94)), rat (ITAGAKI (83)). With greater concentrations decrease in amplitude is recorded in the cat and dog (KEHRER (80)), the mouse (ADLER (100)), rabbit (OKAMOTO (94)), rat (ITAGAKI (83)); and inhibition in the rabbit (FRANZ (108)) and a recently pregnant guinea-pig (HOLSTE (17)). Very little effect was sometimes found in the cat (BACHMAN and LUNDBERG (90)) and in the rabbit (RÖHRIG (35), FRANZ (108), KURDINOWSKY (109), CUSHNY (88), OGATA (46)).

(6) *Nicotine*.—The action of pure nicotine (1:5000–1:1000) upon the uterus was studied by me in five non-pregnant rats. It was found to be inconstant. In some strips very little response occurred, in others an inhibitory and more frequently an augmentor effect was recorded.

In the uterus of the guinea-pig (two non-pregnant and one pregnant) only a slight augmentor effect was observed with solutions varying in strength from 1:10,000–1:1250.

The action of nicotine on the uterus of the rat and guinea-pig thus seems to be similar to its action upon ganglia—first a stimulation and then a paralysis.

Other workers report in some cases an augmentor effect, *e.g.* on the non-pregnant cat (CUSHNY (88), KEHRER (80), FARDON (82), OKAMOTO (94)); the pregnant cat (CUSHNY (88)); the human subject (FRANZ (101)); the guinea-pig *in situ* (SUGIMOTO (102)); the rabbit isolated (OKAMOTO (94), OGATA (46)), and,



*in situ* (CUSHNY (88), FRANZ (108)). No effect on the guinea-pig (DALE and LAIDLAW (14), SUGIMOTO (102)); inconstancy on the non-pregnant cat *in situ* (DALE and LAIDLAW (14)); variation with dose in guinea-pig and cat (HAKAN (110)) and rat (ITAGAKI (83)).

(7) *Ergotoxine or Ergotamine*.—In experiments upon the rat a slight increase in tone, amplitude, and rate was produced by ergotoxine (1:2,500,000). (The ergotoxine phosphate was very kindly given by Dr Dale.) An augmentor effect also followed the treatment of the uterus with ergotamine tartrate (1:100,000) (Ampulles Santoz Chemical Co.) In the non-pregnant guinea-pig ergotamine tartrate (1:1000) produced slight augmentation.

These results agree generally with the previous work done upon the uterus of the rat (DALE (116), SPIRO (118), ROTHLIN (115)) and the guinea-pig (ROTHLIN (115), CLARK and BROOM (117), DALE and SPIRO (116)). SPIRO (118), however, has shown that this augmentor effect in the guinea-pig is confined to the upper half of the uterine horn, a relaxation occurring in the lower cervical end of the horn. TATE and CLARK (125) found that ergotoxine produced no action or relaxation unless the uterus had been rendered excitable by the application of drugs. Both the rat and the guinea-pig are relatively irresponsive to ergotamine and ergotoxine. This may be partly due to the preponderant activity of the inhibitory mechanism in these animals. An augmentor effect has also been recorded in the virgin non-pregnant monkey (DALE (87)); in the human uterus (SPIRO (118)—ergotamine); in the rabbit (DALE and BARGER (113), DALE (117)—ergotoxine, ROTHLIN (114), (115), (117), (122), SCHEGG (121)—ergotamine); in the cat (DALE and LAIDLAW (14)—ergotoxine, ROTHLIN (115)—ergotamine, DALE and SPIRO (116)—ergotamine and ergotoxine).

(2) *The Action of each of these Drugs on the Horn of the Rat with and without the Ganglion.*

The action of these drugs on the isolated horn with and without the cervical ganglion was next studied.

(1) *Barium* caused an increase in the tone and an increase in the rate of the contractions. The presence or absence of the ganglion attached to the strip did not affect the degree of the increase in tone or in the rate of the contractions, nor did it alter the change in amplitude, which increased with weaker and decreased with stronger solutions of barium chloride.

(2) *Adrenaline* always caused inhibition. The intensity of the inhibition produced by adrenaline was not modified by the presence or absence of the ganglion attached to the horn.

(3) *Pilocarpine* produced very little effect on some strips, but an augmentor response was its more frequent sequel. In two pregnant rats, however, inhibition resulted.

The nature of the response to treatment with pilocarpine and the extent of the change produced did not depend upon the presence or absence of the ganglion. In the two pregnant rats in which a decrease of the tone and of the rate and amplitude of the contractions occurred, this inhibition was seen only in the horn attached to the ganglion in one experiment, and only in the one unattached to the ganglion in the other.

(4) *Physostigmine* caused most frequently an increase in tone and in the rate and amplitude of the movements. Larger doses produced an inhibitory effect. The presence or absence of the ganglion attached to the strip did not affect the character and degree of the effect (fig. 15).

(5) *Atropine*, except in very strong solutions, produced an increase in tone associated with a decrease in amplitude and an increase in the rate of the contractions. The response to atropine was not modified in its degree or character by the presence of the ganglion.

(6) Whether *nicotine* produced very little response, an inhibitory or an augmentory

one, the intensity and nature of the change did not depend upon the presence or absence of the ganglion.

(7) *Ergotoxine or Ergotamine*.—The slight augmentor effect following either ergotamine or ergotoxine occurred irrespective of the presence or absence of the ganglion.

#### CONCLUSIONS.

No evidence has been obtained of the cervical ganglion having an autonomic action in controlling either the tone of the uterine muscle or the rate or amplitude of its movements, and, by a process of exclusion, we are therefore led to surmise that the control of the uterine movements must be maintained by the intramuscular neurons.

#### III. SUMMARY.

1. In the rat, guinea-pig, and mouse the sympathetic nerve-fibres supplying the uterus and vagina pass down the hypogastric nerves to the level of the cervix and then pass to the tubes, uterus, cervix, and upper portion of the vagina by several branches. These branches are intimately associated with branches of the uterine artery.

2. Nerve-cells are scattered along the hypogastric nerves and are specially numerous on the course of the hypogastric plexus opposite the cervix. On each side they form a ganglion, the cervical ganglion, which is largest and most circumscribed in the rat, and least so in the mouse.

3. Within the wall of the uterus in these three types of animals, no cells have been found comparable in size, shape, or staining reaction to the nerve-cells found on the more proximal portions of the sympathetic nerve-fibres.

4. The rate of the contractions occurring at the ovarian end is quicker than at the vaginal end of the uterine horn.

5. A comparison of the action of uterine horns connected and not connected with the cervical ganglion, the absence of any effect on removal of the ganglion, and the absence of any difference in the response of the uterus with and without the ganglion to various chemical substances seem to indicate that the ganglion does not exercise a direct influence in controlling the tone and movements of the excised uterus. The point of origin of the impulse controlling the tone and movements of the uterus appears to lie within the uterine wall itself.

The evidence for the action of the intrinsic nervous structures in the uterus will be dealt with in another paper.

I wish to record my sense of great indebtedness to Professor D. NOËL PATON, under whose constant supervision this work has been carried out; also to thank Professor BRYCE and Dr NORMAN MACLAREN for a number of new-born guinea-pigs, and for the use of the projection-microscope in the Embryological Department; and Mr JONES of the Public Health Department, Glasgow Corporation, for wild rats.

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XXIII.—The Expedition to the South Pacific of the S.Y. "St. George."\* Marine Ecology and Coral Formations in the Panama Region, the Galapagos and Marquesas Islands, and the Atoll of Napuka. By Cyril Crossland, M.A.(Cantab.), D.Sc.(London), F.Z.S., O.N. Communicated by Professor W. C. M'INTOSH, M.D., F.R.S. (With One Plate and Eleven Figures in the Text.)

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Two contrasted oceanographical regions are dealt with in this paper, the fauna of the eastern Pacific being distinct from that of the Marquesas, which are the farthest outliers of the western ocean. In each of these two regions again are two divisions of markedly different ecology, physical conditions in the Galapagos being as great a contrast as could well be to those of the coast of Panama, while the Marquesas Islands differ from their neighbours farther west, which are either atolls, or high islands surrounded by broad reefs, in being without coral deposits of any considerable size, and certainly no true reefs. The corals afford a striking example of the contrast between the two main regions; in Panama the only abundant coral is *Pocillopora*, in the Marquesas the only "reef" is of *Porites*, and the other deposits depend upon this genus for their existence. Several species of *Pocillopora* are abundant in the Marquesas, but are all distinct from those of Panama.

Some collecting was done on the Atlantic side of the canal, but my contribution to the problem of the isthmian division of faunas is the considerable material brought from the Panama (or Pacific) side and the Galapagos Islands, while to the problem of the faunas of oceanic islands some data are provided by the littoral collections made in the Marquesas, and, later, in Tahiti.

#### PANAMA—THE ISTHMUS.

The Panama Canal is the most wonderful contrast to that of Suez, with which most of us were familiar, green lawns and tree-covered hills in place of the salt flats and desert, but what more concerns the marine biologist is the fact that this canal is of fresh water throughout, ships in transit being raised by locks to a height of 80 feet above sea-level; there is, therefore, a flow of water from the great central lake to either ocean whenever a vessel is passed through. The natural overflow from the lake passes by the main river of the isthmus to the Atlantic at some distance from Colón, and there are continual flows from the locks to the Pacific. The canal, therefore, in contrast with that of Suez, allows no intermingling of the faunas of the two oceans, unless, among the species which attach themselves to ships' bottoms, there are any which, by closure of shells or opercula, can survive the three to five hours' passage through fresh water.†

The geological history of the isthmus has been summarised by Professor WAYLAND VAUGHAN, who finds that the principal tectonic lines of the Caribbean and Isthmus region existed at the close of the Palæozoic. During later Eocene and middle and upper Oligocene

\* For popular accounts of our voyage see (1) DOUGLAS and JOHNSON, *The South Seas of To-day*, Messrs Cassell, 1926, 21s. (2) C. L. COLENETTE, *Sea-girt Jungles*, Messrs Hutchinson, 1926. Both popular and scientific accounts of Tahiti are in preparation by the present writer. Short preliminary accounts have appeared in *Discovery*, of the present voyage, November 1925, of Tahitian coral reefs, July 1927, and in *Nature*, April 23 and July 2, 1927.

† Cf. Fox, H. M., "Cambridge Expedition to the Suez Canal," *Trans. Zool. Soc.*, 1926.

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there was extensive submergence in the West Indies and interoceanic connection through a number of straits across Central America, the maximum submergence being in the middle Oligocene. Vulcanism was widespread in Central America and the Antilles during Eocene and probably during earlier Oligocene times.

During older Miocene time apparently there was in places connection between the oceans, but these were seemingly restricted, not of wide extent as in the upper Eocene and Oligocene times. That there was in some place interoceanic connection subsequent to the lower Miocene (Burdigalian) is suggested by the presence, in California, of a coral fauna of post Miocene affinities, probably of Pliocene age, since the coral genera *Stylophora*, *Pocillopora*, *Pavona*, and *Goniopora* (to mention the more important of Professor VAUGHAN's list) are absent from this Californian deposit, but survive in the Pacific, *becoming extinct in the Atlantic during upper Miocene time*.

In the Mesozoic VAUGHAN gives only "possible" and "probable" connections.\*

The following valuable information on the passage of fresh water through the canal, and the effect upon the organisms which attach themselves to the bottom of ships, has been given me in a letter by Mr R. Z. KIRKPATRICK, the Chief of Surveys: "During the calendar year 1925, 558 cubic feet per second of fresh water entered Limon Bay through the Atlantic locks; almost exactly the same amount came into Panama Bay from the Pacific locks. Approximately 3550 cubic feet per second of fresh water entered the Caribbean through the old mouth of the Chagres River, being the water spilled over Gatun spillway and used by the Gatun hydro-electric for power. However, the mouth of the Chagres River is about six miles south-west of the Atlantic entrance to the Panama Canal, and in no way could be presumed as a factor in density and temperature at the Atlantic entrance. Density determination ranges have run:

Cristobal (Atlantic side)	1.019 to 1.026
Balboa (Pacific side)	1.010 to 1.024.

*Note.*—Minimums at low tide and considerable down lockages; maximums at high tide.

"Sea temperatures:

Cristobal	75° to 86° F. at 10' depth
Balboa	†60° to 86° F. at 10' depth.

"The fresh-water passages through Miraflores and Gatun Lake as regards effect upon ship-bottom marine growths and barnacles have been a disappointment. In the ordinary transit but three to five hours of fresh water is encountered—no appreciable effect is noted. Even dead growths have to be dislodged by mechanical means; several ships which for various reasons have remained in Gatun Lake for considerable periods of time still show dead growths in place.

"You may be interested to know that sea-borers have evolved (apparently during the short life of the Panama Canal) so that they now live in Miraflores Lake between 100 to 1000 parts salinity in one million. (See *Neoteredo miraflorea* and *Bankia zeteki* of Bartsch, 'Marine Piling Investigations,' National Research Council, Washington, D.C., also 'A Monograph of the American Shipworms,' by PAUL BARTSCH, *Bulletin No. 122, U.S. National Museum*."

On the above we may note that we have still to determine how much of the fauna of a

\* T. WAYLAND VAUGHAN, *Bull. Geol. Soc. America*, vol. xxix, pp. 615-630, 1918.

† During cold-water period only (January to April); during remainder of the year 76° to 84° F.

ship's bottom remains alive and therefore has a chance of establishing itself on the other side of the canal. From the point of view of the ship-owner a dead organism attached to the bottom is as great a retardation of the ship's speed as is a living one, but it seems possible that such dead shells, etc., may drop off after the vessel has been a few days in the ocean, together with any young growths which have attached themselves to the old in the meantime. Further investigations on these points might yield interesting results both biologically and commercially.

Certain Polychæte worms (an ancient group) are widely distributed and are found on both sides of the isthmus. Collections not yet being worked out, three of the more striking examples may be quoted. A *Panthalis* (Aphroditid with a flabby tube of mud and mucus) was obtained at Trinidad and Colón in the Atlantic. The worm emerging, displayed a beautiful and characteristic coloration, the dorsal scales being primrose yellow edged with black. This species was obtained again at Colón, the Atlantic entrance to the canal, but on the Pacific side another species with a distinct colour scheme. This seemed like a beautiful example of the distinctness of the Atlantic and Pacific faunas, but further work showed that it was only an instructive example of the danger of founding generalisations on small collections, as later the Atlantic form was found here also. Possibly the Polychæta, being an ancient group, are more widespread than others, several species on this voyage seem to have been found at every point we touched at, e.g. the little *Lumbriconereis*, which I obtained in the Cape Verdes in 1905 and named *L. albifrons* in 1924,\* is common both in the Marquesas and Galapagos (obtained only from "washings" in both cases, as it was in the Cape Verde Islands). One of the most curiously coloured of worms is a species of *Leodoce* (*Eunice*), which is uniformly of a deep violet with a clear white collar and white rings on tentacles and cirri. This was described by CLAPARÈDE from the Mediterranean long ago, and was seen again in the Cape Verde Islands by me in 1904, where I found it only among the encrusting organisms under barges. Searching the floats under a floating pier end at Taboga twenty years later, the same species was obtained in the Pacific. It is just possible that this form has been transported in the fauna of ships' bottoms.

As conspicuous examples of the differences between the two sides of the isthmus we may quote the corals and the faunas of the docks at Colón and Balboa. The former is well known, but as the *absences* from the Atlantic coral fauna have generally been emphasised it may be as well to remember that the fauna of the Panama region is very much the poorer, the only abundant genus being *Pocillopora*, and probably only one species of that, *Porites* rarely of any importance and *Pavona* rare, while the Galapagos, with their entirely different conditions, only add one or two other members.

The docks at the two ends of the canal are similar and under much the same physical conditions, except that while there is no tide at Colón there is at Balboa. In the abundance of fresh water and scums of tarry oil they are alike, yet both support an abundant fauna, the piles of the wharf at once attracting attention. At Colón these were thickly covered with the bivalve *Perna*, a quantity of which being scraped off and examined in the laboratory yielded a large number of animals, apart from the accompanying *Ostrea*, *Mytilus*, sponges, ascidians, polyzoa, and hydroids. Weed is also abundant on the floating fenders of timber which line the dock sides, whereas on the Pacific side, though there is abundance of hydroids and polyzoa, *there is no weed*. The piles in Balboa show the same zones of life as does the open shore, viz. rock oysters above, below this *Balanus*, and at lowest tide level hydroids

\* *Proc. Zool. Soc.*, 1924, "Polychæta of Tropical East Africa, the Red Sea, and Cape Verde Islands, collected by CYRIL CROSSLAND, and of the Maldive Archipelago, collected by Professor STANLEY GARDINER, M.A., F.R.S."



and polyzoa. The thick growths of *Perna* and accompanying bivalves, which are the features of the piles at Colón, are absent. (This might conceivably be due to the swarms of a little spiny *Diodon* in the Balboa docks, which lives upon young shellfish among other things, so that even if the spat of *Perna* settled upon the piles it would be all browsed away.)

The absence of weed was found to characterise the whole region, wherever we explored it, and reference to the map shows that we extended our journeys well to north and south of the Gulf of Panama, to Coiba in the north and Gorgona southwards. While the rocks at low tide below the city are golden with a mossy growth, this is a Sertularian Hydroid, there is no weed at all, but a painting of some of the pools with encrusting lithothamnia, while others are gorgeous with vermilion sponge. Similarly the shores of the islands had but this same painting of the boulders at low-tide level, and a little conferva, but plant life is practically absent. (Inconspicuousness of weed is a usual feature of tropical shores, but it is always present, though not in the bulk usual on northern shores.) Its absence here may be connected with the peculiar conditions prevalent, the almost perpetual rain and dull skies, the extreme muddiness of the water, largely due to the vast quantities of vegetable matter, from leaves to whole trees, which are brought down by the westward flowing rivers, and which are continually met with out at sea and along the shores, and to the almost perpetual calm. The absence of gravel at high tide and the sharp edges of the stones below show that no surf ever disturbs the shore; a consequence is the accumulation of mud, the "almost unbelievable mud" of Agassiz' description. This is largely organic, and at Panama hides the bottoms of pools a foot or two deep, while, even off the islands 20 miles to sea, visibility extends but to one or two fathoms. Mud covers the sea bottom everywhere, inshore and off the islands, with the exception of some accumulations of shells and shelly sand near the Perlas Islands and Jicaron, the southern extremity of Coiba. And yet a fauna of great richness can flourish.

The littoral fauna is in fact the richest I have met with, but is not to be found everywhere. The reef of mingled lava flows and soft shale beds, below Panama city, is an area of great richness, but much of the shores of the islands we visited is of rounded boulders and sand, from which little can be obtained. Collections were obtained from Balboa Docks and Panama, Taboga, and Perlas Islands in the Gulf of Panama, Coiba and Jicaron Islands to the north, and Gorgona to the south.

On the mainland near Panama there are no reef-forming corals, but little clusters an inch or two across, with pink or rose coloured polyps, are common under stones. The larger vermilion or orange *Dendrophyllia* with the same habit is not found here, though it is common at all the near-by islands as well as the Galapagos, Marquesas, and Tahiti. It is never a reef builder, living in crannies and under shelves of the rocks above the level of lowest tides; it is not intermingled with the *Pocillopora*, which is never exposed. In the deeper pools in the lava at lowest spring tide small Gorgonians are abundant, several species being sometimes present in the same pool. This was a novelty to me, as on the coasts I have seen "sea fans" were obtained by dredging only, and then as rarities, whereas the fleshy Alcyonaria, here totally absent, abound in extraordinary numbers on most tropical shores.

Of the Polychæte worms, as stated, an abundance of both individuals and species is to be found right up to high-water mark, where the black sulphurous-smelling sand is crowded with a Spionid. In the lower pools the giant Sabellid *Spirographis*, with its spiral of feathery plumes, is abundant; *Diopatra* with its peculiar tubes built of shell fragments, or any other material available, e.g. twigs and dead leaves, is common from low to high tide. The genera of Terebellidæ were numerous and varied, but the largest worm tube I ever saw is made by

a simple *Eunice*, whose tubes are of mud, standing vertically a few inches above the sand, with their tops turned over horizontally with a narrow opening. The worms are difficult to secure, as the tubes pass through the sand among the stones beneath, but one of the larger, over an inch thick, which, owing to the presence of a flat rock was forced to run horizontally, was followed for 3 feet and then only the anterior end of the worm was secured. Of the

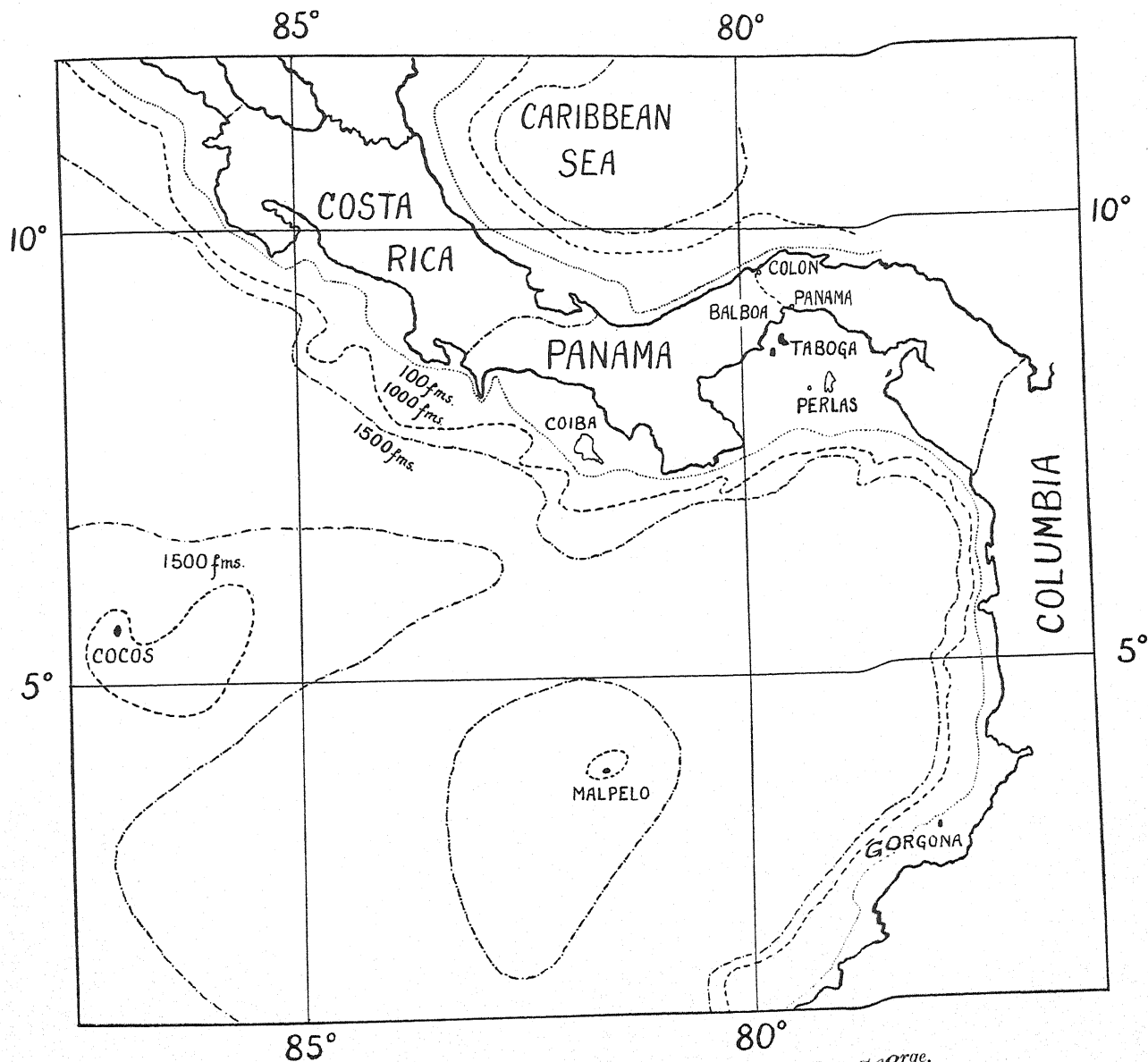


FIG. 1.—The Isthmus of Panama and the localities visited by the S.Y. *St George*.

errant forms, I was especially struck by the agility which a *Chlorhæmid* (in spite of the gelatinous consistency of the perfectly transparent body) showed when *its* shelter under stones, in which half a dozen specimens hid together, was disturbed; a *Lumbriconereid* possessed "gills," this genus being characteristically without these structures; the species is new, not the West Indian *L. branchiata*. Besides the Sertularian mentioned as giving a golden colour to the rocks, other Zoophytes, both hydroid and polyzoa, were *ex*ceptionally varied and numerous. Experience of the other beaches of the Panama region shows that the richness of this is exceptional, and largely due to its geological formation.

The corals of all this region are of few species, one or possibly two of *Pocillopora* greatly predominating. *Porites* is rare, *Pavona* is seen only occasionally, while *Psammocora* occurs as loose nodules. There are no true coral reefs, and the existence of the deposits which occur seems to be due to a minimum rate of decay and the perpetual calm of the region. Scattered growths of *Pocillopora*, such as in the Red Sea would have no effect on accumulation, have here produced considerable quantities of material, all of which remains loose. The beach is often covered by coral carried up by the feeble waves of this sea, but in any less pacific region, not a proportion, but the whole, would be thrown on to the shore by the first gale.

Taboga Island, 9 miles out in Panama Bay, shows typical flats along its more sheltered eastern side. These are composed of the debris of a rather fragile species of *Pocillopora* just below low-tide level along most of the east or leeward side, but the rocks on the other side of the island descend straight into the water. There are larger colonies of *Porites*, but these are too few to make any appreciable proportion of the deposit. In general the surface of the flat consists of dead pieces of *Pocillopora* covered with *confervæ* above and encrusting *lithothamnia* below, but the latter fails to cement the pieces together. The coral living on this flat is often found to be due to the continued growth of branches thrown up from its edge, growing as a plant may grow from a cutting. The edge is steep and in places covered with *Pocillopora* as thickly as it can grow, but only for a fathom or so down, dredging below this level bringing up coral fragments only, generally bound together into lumps by a yellow-green sponge and *Lithothamnia*, and in contrast with the material from the flats, rich in animal life of all sorts. Below this, in water as shallow as 5 fathoms, is the usual thin mud of the region, and, with the exception of the Perlas Islands given above, this was the rule. This island illustrates again the dependence of the littoral fauna on geological structure and shelter, as here the only area of shore with much life is the spit of beach sandstone between Taboga and Morro Island. Elsewhere rocky and sandy shores alike are comparatively barren.

At Gorgona coral growth is limited in a similar way, though a few other species are found with the dominant *Pocillopora*, and beaches half of coral are more extensive. Even so far from the mainland the coral debris below the shallow growing zone passes into soft mud, which covers the whole channel, here at its deepest, 30 fathoms. These islands are at all times like oversaturated sponges, water seeping from them at other points than the mouths of the numerous streams, which, as is so often the case, have no visible effects on the corals near them.

Coiba Island has the largest accumulation of coral seen, just below the convict settlement, which is the only habitation on the island. Here the beach is gravelly, with much rolled coral, shells, etc., and overturned trees on the little flat between the sea and the slope behind expose the same among their roots. At low-water level the dead coral is bedded in the sand to form a level surface, of which cylinders of *Porites* are for the first time important, and many show the effects of the gradual advance of the sand upon their growth before they were finally killed. Living coral is abundant at a level about 2 feet lower and some distance seawards, forming an offlying patch. This consists of the usual abundance of brown *Pocillopora* with a few large colonies of *Porites*, and one comparatively solid mass of *Pavona* was found. Below this is a slope of coral debris, and above a flat of broken coral, sand, and thin mud. Even after prolonged calms the water of the reef was opaque with red clay in patches, such as is usually supposed no corals can survive.

The bottom at 5 fathoms shows that storms are hardly known, as it is composed largely of a finely branched *Lithophyllum* in loose pieces 2-4 inches in diameter, with quantities of



red weed attached to them. Sponges of several species form loose balls 1-3 inches in diameter; they show a core of small pieces of *Lithophyllum*; there are also scattered leaves of a *Pavona*. Mollusca are numerous, especially *Murex* and *Turritella*; the shells were often covered with hydroids and polyzoa, but these were not present on shells occupied by hermit crabs.

This history of this coast is easily read. Comparatively recently the slopes behind the narrow band of flat land were marine cliffs, beneath which corals flourished, making a more continuous and solid deposit than is usual in these seas. There was a change of level of about 2 feet, the cliff of soft rock became a slope, both slope and flat being now under cultivation; the corals were slowly buried and growth transferred farther out to sea, forming a little barrier shoal a hundred yards out.

Corgona recalls Taboga in its coral deposits, living coral of the usual species, forming a band a fathom or so deep, not covering the whole surface, yet its debris accumulates more

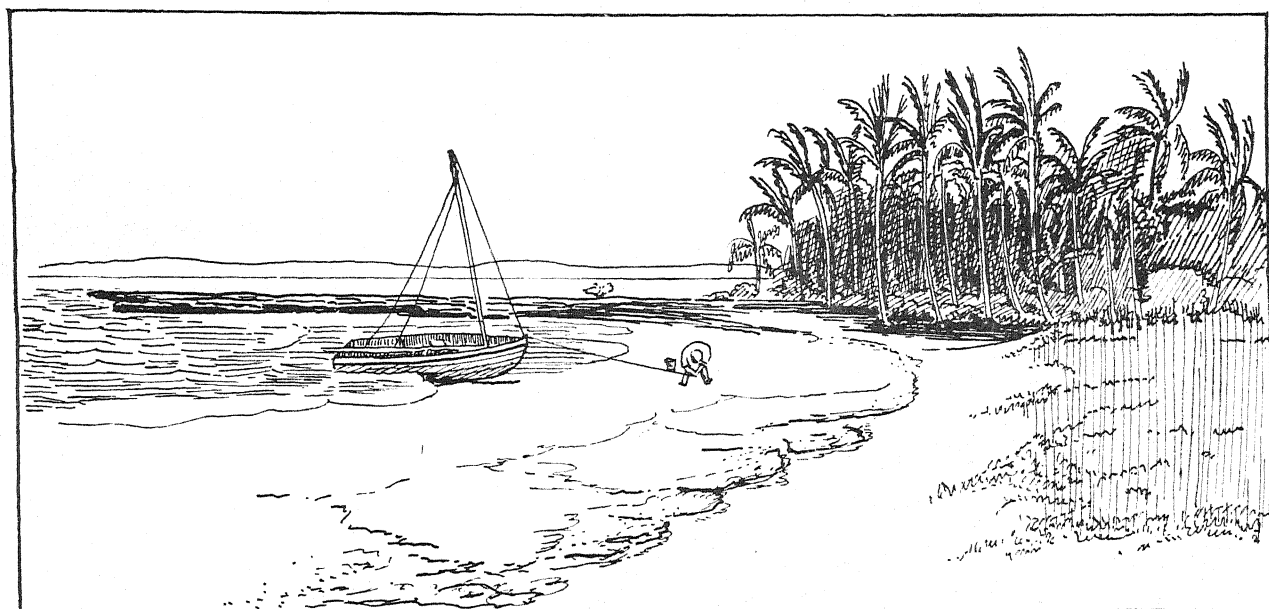


FIG. 2.—Coral reef and Halimeda beach of Limon Bay, Colón, on the Atlantic side of the Isthmus.  
From a photograph by L. J. CHUBB.

rapidly than it is removed and extends as deep as 15 fathoms, but no solid rock has formed anywhere. An additional coral genus occurs here in solid masses 3 or 4 feet each way, of which I was unable to obtain specimens owing to the incapability of my diver. The coral debris appeared at first sight to be rich in polyzoa and sponges only, but narcotisation liberated a large number of animals of many other kinds. Otherwise collecting yielded little, either ashore or by dredging. Coral everywhere affords a habitat to fish and crustacea among its branches, here more abundantly than usual. On one occasion some natives brought five fair-sized colonies of *Pocillopora*, from which 2-3 lb. of relatively large fish and crustacea were washed out, besides multitudes of smaller crustacea and worms. Here fishes of the strange forms and brilliant colours, usually associated with a coral sea, were more in evidence than at any other place we visited, Tahiti not excepted. In spite of the abundance of mollusc-eating fish, the Panama pearl oyster, *Pinctada margaritifera* var. *mazatlantaca*, is common both above and below low water, but is not fished hereabouts. Most of the shells are heavily parasitised, few reach more than 10 cm. in diameter, and this variety of the species has a market value below even that of the Red Sea.

Dredging in 30 fathoms, on a bottom of fine mud, was tedious, but yielded a fair number of species of Polychæta not seen elsewhere. This may be connected with the extraordinary coldness of the mud,  $15.1^{\circ}$  C. at 25 fathoms when the surface temperature was  $26.5^{\circ}$  C. The latter was always high enough for coral growth, being between  $25^{\circ}$  and  $26.6^{\circ}$  C., but it is possible that temporary northern extensions of the cold South American current may cause lowerings of temperature fatal to most species. Owing to the steepness of the slope off this side of Gorgona the low bottom temperature recorded above was only a few yards away from the growing coral. On our crossing to the Galapagos we found the lowest surface temperature was  $20.7^{\circ}$  C. ( $69.2^{\circ}$  F.).

The contrast between these deposits and the reefs of the Caribbean is illustrated by the example of the latter in Limon Bay, near Colón, of which I give a drawing from a photograph by Mr CHUBB. This consists of a flat, slightly above sea-level, but covered with living lithothamnion and a little *Porites* and *Millepora* at its edge. The rock is typical hard coral rock, made up largely of "brain coral," a type seen nowhere else on the voyage nor in Tahiti, the colonies *in situ*. The surface was planed down, exposing sections of the contained corals, during a pause in the movement of elevation, and in spite of the vigorous growth of lithothamnium, the edge is not growing, the fissures which so resemble spaces between outgrowing tongues in other reefs here being the results of erosion. The beach sand is largely from the abundant growth of *Halimeda*, an alga which was not seen again until the Marquesas were reached.

#### THE GALAPAGOS.

These are volcanic islands in practically their fresh condition. They were especially interesting as affording a basis for comparison with the eroded volcanoes of the Society, and the still further reduced Marquesan, Islands. Each island of the Galapagos is formed of a complicated set of volcanic vents, in most a main volcano with lesser cones on its flanks, either perfect, eroded, or broken by explosions, while offlying islets may have no obvious relation to the cones at all. In contrast the Society Islands consists of simple cones with no subsidiary vents, and no outlying islets of volcanic origin, and some of the Marquesas have double cones broken by great earth movements. The differences and likenesses between the shallow water faunas of the Galapagos and Panama may be due to geographical conditions, but the whole ecology is a contrast to that of the mainland. The clearness of the water permits visibility to a depth of 10 fathoms; weed is abundant and varied, *Sargassum* hanging from the rocks at low tide as *Fucus* does in temperate regions, in marked contrast to the general condition in the tropics, where such weed is sparingly found. Lithothamnium are not abundant at James Bay, more so at Conway Bay, and quite plentiful at Post Office Bay. A further difference is seen in the beaches, that at the first bay being purely of broken shell, at the second of shells and volcanic sand, at the third principally volcanic. At Post Office Bay, just below low-tide level, are quantities of nodules of Lithothamnium, usually with a pebble as centre, and a beautiful foliaceous form is not uncommon. Yet even here no considerable masses nor extensive protective crusts are formed, and we doubt the existence of such in the group. Of other algæ, corallines, a large *Padina*, and *Ulva* with small stiff fronds like those of a liverwort, and a stiff mossy green weed were the commonest; the last is remarkable for the amount of animal life it sheltered, including hydroids, nematodes, and insect larvæ.

Evidences of changes of level were conflicting. On the one hand there is a low shelf round some ash island, e.g. Albany Island in James Bay, resembling that which surrounds the Marquesas, parts of Tahiti, Samoa, etc., but this is not general. Certainly many of the

lava flows reached the sea while at its present level. On the other hand there is a partly submerged "peat" bed at Conway Bay, made of the roots of mangroves, of which living specimens grow at the top of the beach. This forms a little flat at low tide but extends beneath the lowest springs, and its condition gives clear evidence of recent, even if local, subsidence.

I myself did not find any corals, either by dredging or thrown up on the beaches, but Mr HORNELL, whose duties took him further afield, found considerable quantities on certain

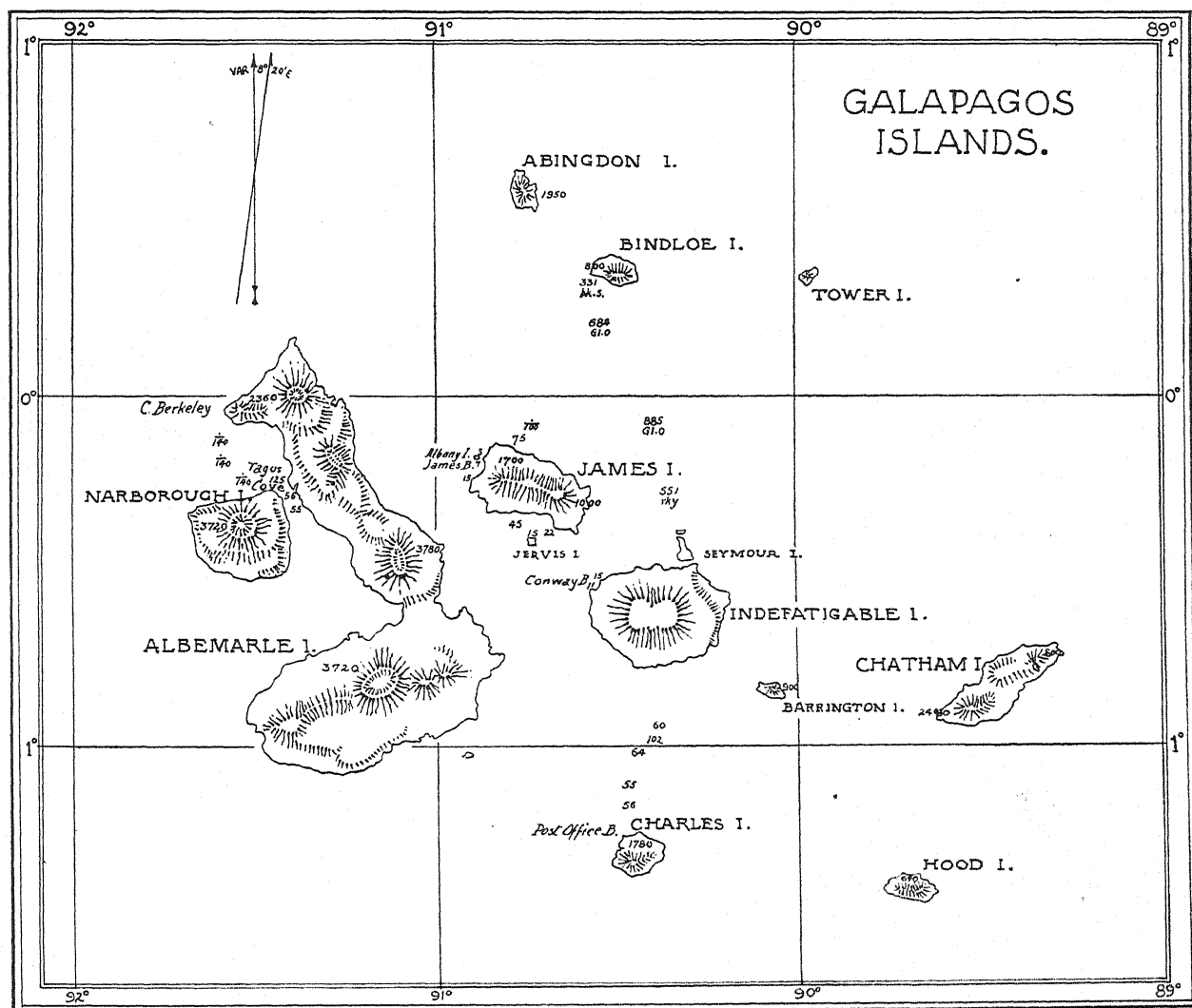


FIG. 3.—The Galapagos Islands, showing the bays visited by the S.Y. *St George*.

beaches. No rock which could possibly be called coral rock was seen by any of us, though AGASSIZ asserts that such rock is characteristic of Galapagos beaches, mentioning especially Conway Bay which we particularly examined. "On nearly all the islands are a number of sandy beaches, made up of decomposed fragments of coral and other invertebrates, cemented together at or beyond high-water mark, into the modern reef-rock I have described." "Conway Bay itself, where we anchored for the night, on Indefatigable Island, is a fine example of one of the coral rock beaches so characteristic of the Galapagos." \*

It is clear that the rock referred to as "coral rock," and "modern reef-rock," is what is generally known as beach sandstone.

\* AGASSIZ, *Amer. Bull. Mus. Comp. Zool. Harvard*, vol. xxiii, 1892-3, p. 64.



Mr HORNELL's notes are as follows:

A. *Coral beaches* :

1. Indefatigable Island. Just beyond the north end of Conway Bay is a high bank of dead coral, of reef-forming facies, and odd blocks are scattered between tide marks.
2. Charles Island. Cormorant Bay has several short beaches of dead coral, in blocks, branches, and smaller fragments, one beach consisting almost entirely of rounded blocks as large as a man's head piled on the lava substratum characteristic of the place, another beach of smaller pieces, the sand adjacent to these beaches partly composed of coral particles mixed with shell fragments.

B. *Recent beach sandstone was seen*—

1. Near the coral beach of Indefatigable Island, but this did not itself contain coral, but contained shell fragments and broken spines of *Cidaris*. The deposit lies in front of the sanded-up entrance to a lagoon.
2. On Charles Island at the east end of Post Office Bay, composed only of shell fragments and particles of volcanic material.
3. At Black Bight, Albemarle Island.

It is surprising to find no more coral growth in these clear waters than in the mud of Panama, if indeed there is so much. AGASSIZ suggests that the erosion of these rocks forms a detritus too small and loose for the attachment of coral larvæ, and considers that the coldness of the water is a less hindrance to coral growth than the spread of silt from the western flowing rivers of Central America. As has been shown, this silt does not reach the *shallow* water round these islands, so that it is clear that the lower temperature is at least as great a detriment as the mud of Panama.

The shores of these three bays visited are largely composed of lava flows enclosing pools at low tide. These support a fauna apparently as rich as that of Panama; certain pools were extraordinarily rich, in one pool no fewer than eight species of Opisthobranch being taken, and in another six different species of Terebellid worms. The submerged "peat" bed is another habitat of special richness in Polychæta, of the Eunicidæ alone there were representatives of the genera *Leodoce* (*Eunice*), *Marphysa*, *Onuphis*, *Lysidice*, *Lumbriconereis*, *Arabella*, and *Dorvillea* (*Staurocephalus*).

It is regretted that our time was too short for complete collections to be made, which would, I think, prove that the shallow water fauna is as rich as that of the continent.

Tagus Cove \* differs altogether from the preceding bays in being a small crater, from which one side has been blown out, admitting the sea. The lava flows of the preceding bays are all low, ending generally in black cliffs a few feet high, which in appearance recall those of raised coral of tropical East Africa, while in Tagus Cove the yellow ash beds of the crater descend directly into deep water, with here and there a ledge only a foot or two wide at low water; there is no access to the land except by one small gully at the head of the Cove. The rock breaks down into a clean sand, and finer sediment is absent, the slight surf removing what little is formed, and the products of algal and animal decay. Shore collecting is surprisingly rich, for so clean is the gravel, in such small pools as there are, that small stones are

\* For a geological description of Tagus Cove and the Galapagos and Marquesas Islands generally, see L. J. CHUBB, M.Sc., "The St George Scientific Expedition," *Geological Magazine*, vol. lxxii, pp. 369-373, August 1925, or his full account in *Quart. Journ. Geol. Soc. London*, 1927.

coated completely on every side by polyzoa, which also cover the algæ half-way up from their bases, and above these there are *Obelia*-like hydroids. Polychæta are abundant, beautiful Sabellids, with plumes of various colours, are numerous, and half a dozen specimens of a red Amphinomid are found under every stone. The bottom of the cove is about 12 fathoms deep, covered with clean, rather coarse, sand. Here again weeds are abundant and varied, supporting a large fauna of hydroids and polyzoa. Sponges are common everywhere, mainly as incrustations; two offlying rocks nearly dry at low tide were completely covered with them. I expected that Lithothamnium would form a continuous protective crust to the rocks about low-tide level,\* at any rate near and outside the opening of the bay, but this was not found here, or anywhere else in the group, either on this soft ash rock or on the hard lava of the other bays. The usual weeds occur, *Sargassum* becoming especially abundant out towards the points.

The climax of this profusion is reached at a point where the cliff overhangs, and protects from the sun a shelf of rock which lies just below low-tide level, making a veritable sea-garden. On a carpet of blue sponge and some Lithothamnium are rounded colonies of scarlet *Filigrana*, which suddenly become white when touched, the little scarlet worms retracting into their tubes, yellow and pink corals (*Dendrophyllia*), with large flower-like polyps, masses of *Tabularia*, and fan-shaped reticulated Gorgonians.† These are below low water, but at that level are two species of branching polyzoa and a beautiful plumularian hydroid (? *Halecium*), while higher up are a varied array of anemones in thousands, and any vacant space is covered with a dark brown encrusting polyzoan. Other sponges, and large masses of compound ascidians, are also abundant. In all my travels I have seen nothing so rich and beautiful, as this surpasses the best coral beds in the variety of the forms which make up the garden. Here, too, were large "acorn barnacles," which interested me mainly in that their empty shells, which are over an inch high, shelter a marine spider, also taken at Post Office Bay. The finding of so incongruous an animal was equalled by centipedes being part of the normal marine fauna at low tide, but I had taken both twenty years earlier at Zanzibar‡ and Cape Verde Islands respectively.

On our first landing the water was milky with teeming Amphipods all the way from the yacht to the shore, but these soon disappeared. They inhabit shore algæ in such numbers that washing out half a bucketful of weed yielded 3 cubic ounces of small animals, mostly amphipods.

An ecological fact of the first importance is the necessity for all marine animals to be provided with some protection against becoming a settling ground for the larvæ of fixed forms. The Gorgonians are supposed to be especially well protected by their stinging threads and mucus secretions, and it was surprising to find the little hydroid *Obelia* growing over the living branches of the species found here, as well as upon a polyzoan. Ophiuroids are the commonest commensals with Gorgonians, here a light blue form sometimes almost covering them, but on washing out a quantity of these "sea fans" they were found to harbour quite a large fauna of more delicate creatures.

In Tagus Bay a bucket full of *Padina* weed was brought into the laboratory for closer examination than is possible in the open, and the result of a careful detailed search was the discovery of five examples of an Aplysiid, about an inch long, coloured so exactly like the weed that its presence was unsuspected until this second examination. Nor was this all, for the weed being put into basins for narcotisation, fifteen further specimens detached themselves. The deception was even more perfect than that of similar molluscs on the grass-like

\* Cf. Crossland, C., "Ecology and Deposits of the Cape Verde Islands," *Proc. Zool. Soc.*, 1905, p. 170.

† This gorgonian is a new species, and is being described by Professor S. J. Hickson under the name *Gorgonia galapagensis*.

‡ Pocock, "A Marine Spider of the genus *Desis*," *Proc. Zool. Soc.*, 1902, p. 389.

*Cymodocea* of Zanzibar and East Africa, and the same thing occurred in Tahiti, an additional species being discovered by adding the narcotising agent to weed which had been already searched. A larger Aplysiid, which in the Panama region is greenish grey with marking of Lithothamnion purple, is in the lava pools quite black. In the same pools are numerous small specimens of the crab *Dromia*, all of which carry the same glossy black compound ascidian, while an *Oncidium* and a *Fissurella* are also of the prevailing colour.

THE MARQUESAS.

We arrived in the anchorage of Taa Hu Ku, Hiva Oa, on December 26 and remained in the group for forty days, visiting the anchorages marked in the islands of Fatu Hiva and

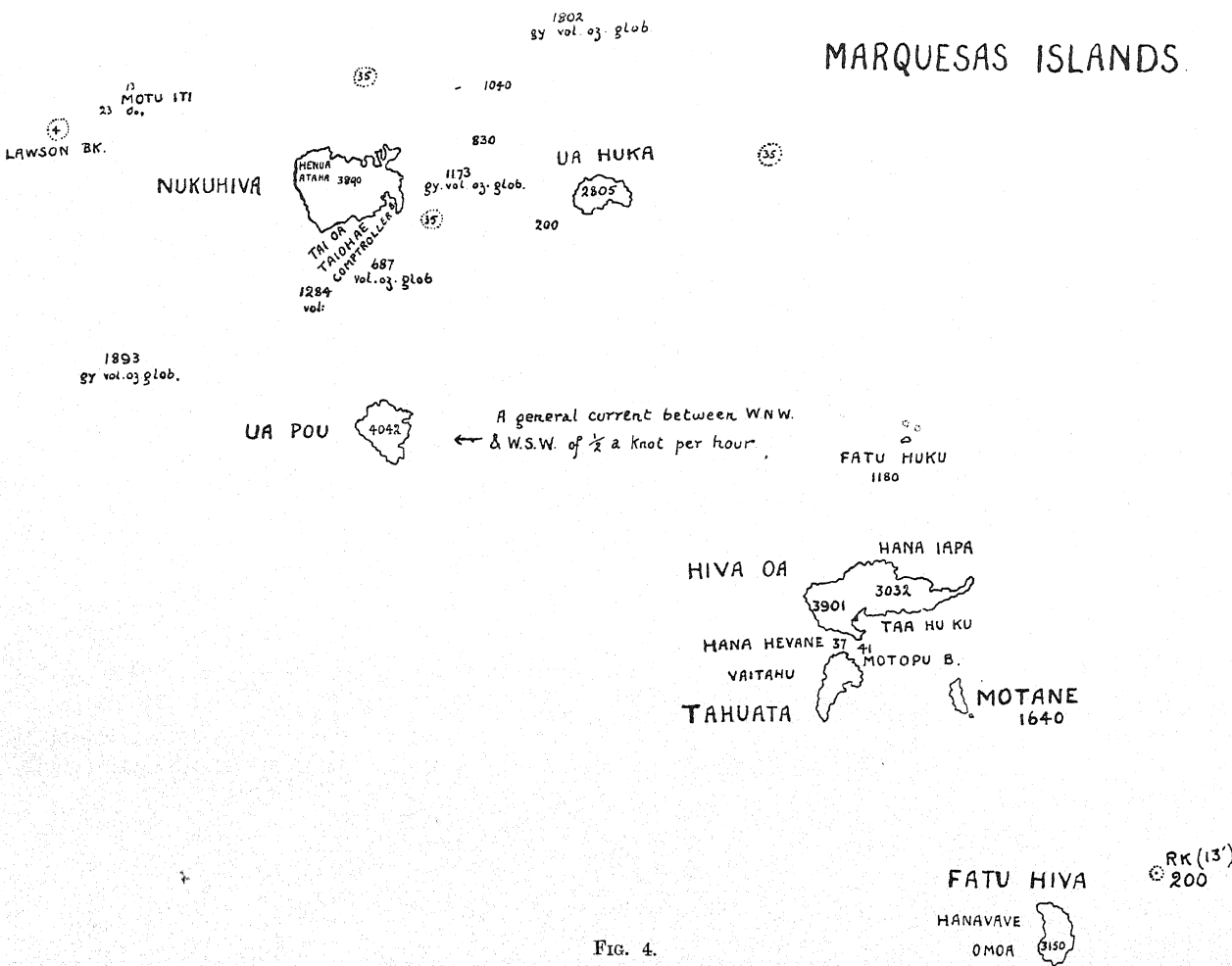


FIG. 4.

Tahuata in the southern group, and Nuka Hiva in the northern, where we saw the famous "Typee" valley of HERMAN MELVILLE.

The beauty of these remote islands, their combination of majestic mountain and cliff with fruitful valley, the melancholy decay of their once numerous and happy people have been described by other members of the expedition. To the marine biologist they are of exceptional interest, the problem presented by the absence from them of any coral reefs, while their nearest neighbours are the atolls of the Tuamotus and the broadly reefed Society Islands, being almost classical in coral reef literature. In the case of these islands discussion



has tended to outrun observation, but fortunately we now have a more complete account of the geology and tectonics by my colleague Mr L. J. CHUBB.

It is clear that there has been heavy faulting in these volcanic islands, and to this the enormous cliffs, 1000 feet high, are largely to be attributed, those due to regular marine action upon volcanic slopes being comparatively low. Some islands consist of half craters, or the halves of double craters, the missing parts having disappeared below the sea. It is possible

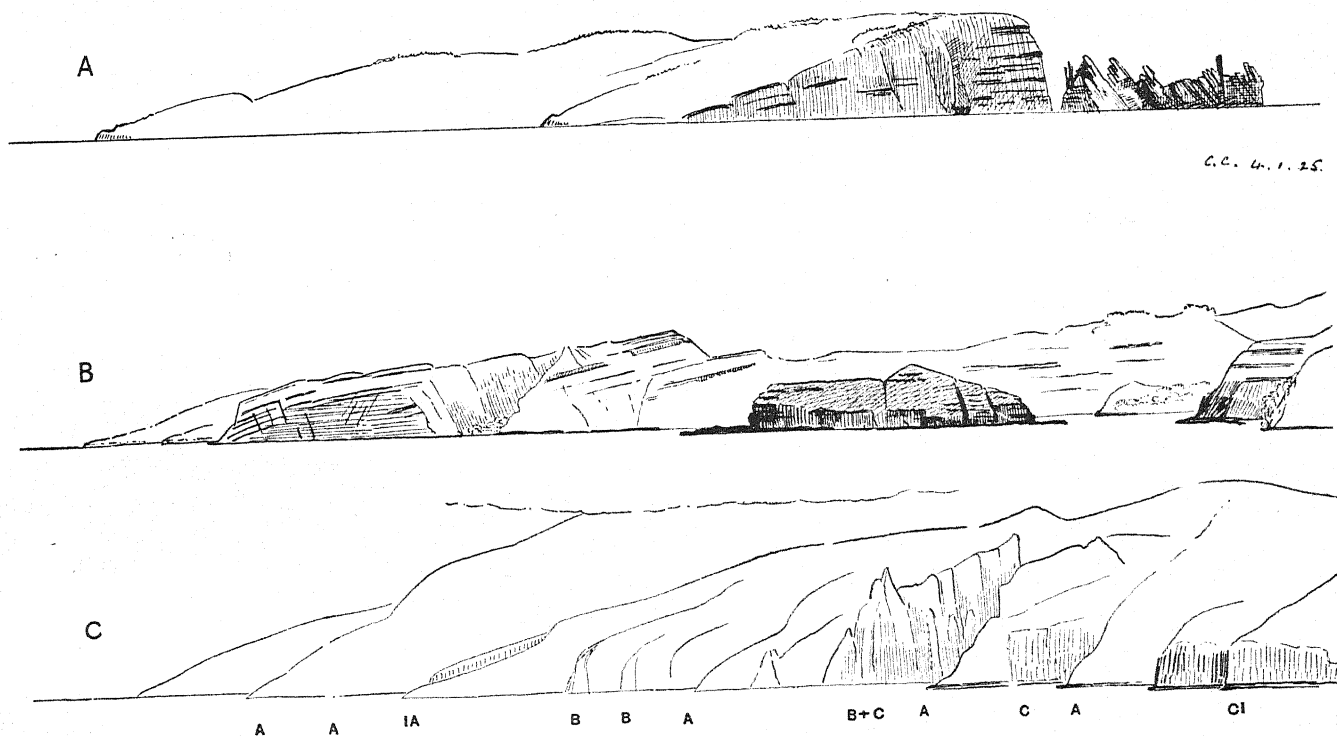


FIG. 5.—Three views of faulted coasts in the Marquesas.

- A. Motane Island bearing N.E., showing trivial marine erosion, the great cliffs and stacks at the south end being due to faulting, there being no more exposure to marine action there than elsewhere. The dips of the strata are clear, horizontal near the crater, following the slope of the island to the north. The southern half of the cone has collapsed.
- B. Hiva Oa Island, looking across Atuona Bay to S.S.W. Compare the plan of fig. 6. Anakei Island shows minor faulting and the maximum development of the shore shelf. The volcanic strata dip seawards only on the hills of the left hand of the sketch, to the right they are horizontal, *i.e.* were laid down near the crater, showing that the greater part of the outer slopes of the cone has disappeared.
- C. The west side of Fatu Hiva Island, showing the independence of coast form to marine action. These forms comprise (a) spurs running into the sea without conspicuous cliffing, (b) spurs ending in triangular cut-offs, (c) cliffs of great height distinct from the lower sea-cut cliffs. The high hills with cloud-covered tops are the remaining part of the original great crater, the lower dissected mass, all to the right of 1A, the half of the secondary crater formed within the first. On the hillside above 1A are great cliffs, but none by the sea. The shore shelf is seen at the bases of the nearer sea-cut cliffs on the right.

that coral reefs could not be formed upon such deeply faulted coasts; \* but this faulting affects only one side of some of the islands, and even the small number of soundings we have show quite suitable depths for the foundations of coral reefs in many places, and the high cliffs have a considerable amount of talus at their bases.

No raised reefs whatever were found, and it may be taken that they do not exist. Later movements show a submergence by which the river mouths were drowned to depths of 300, 400, and 600 feet, followed by an emergence, shown by the shore shelf which runs round the bases of practically all the cliffs. This is so regularly found, at about the same level, in so many places in the Pacific, that it seems certain that the ocean has sunk at least 6 feet.

AGASSIZ suggests that the character of the sand formed from erosion of these hard rocks

\* But cf. the Red Sea.

makes a substratum upon which coral larvæ cannot settle. It will be seen that this is one adverse influence, but certainly not in itself prohibitive. Since the date of his paper observations on the foundations of reefs have been made in various parts of the world which make this hypothesis \* unlikely. To mention only the Red Sea, elevated reefs there may rest directly upon, or with only an inch or two of shelly matter intervening, (1) soft sandstone, (2) coral mud, (3) gypsum. They are recent shallow water reefs, and the corals are in the position in which they grew, not broken pieces carried from other reefs on to these soft, loose, and soluble substrata.†

The view that reefs are absent because there is no broad platform of erosion upon which they could have been built cannot be fully proved or disproved until many more soundings around the group are available. In any case, that the problem is ecological rather than geological, even a cursory examination of the coral fauna shows. Many of chief reef-building corals do not occur, and those which do exist attain their full development only exceptionally.

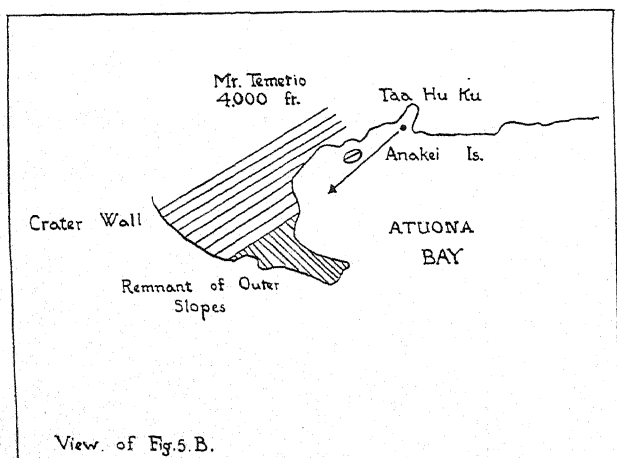


FIG. 6.

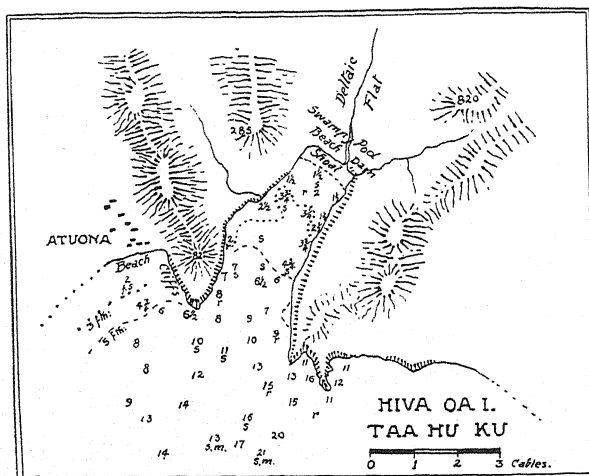


FIG. 7.

All our anchorages were fundamentally alike, a short bay with rocky sides and a short beach at its head, the small embayments of the valley mouths, such as is illustrated by the plan of Taa Hu Ku. The surf penetrates to every part, and the beach is of sand, gravel, and boulders, generally a combination of the three, which has been thrown up as a dam across the stream mouth, forming a pool, which adds much to the romantic appearance of the villages. The black basalt cliffs in the bays are not very high, and here, as outside, a rock shelf runs along their bases above high-tide level, as shown by patches of grass on its landward side, though seawards there are often pools kept fresh by the surf and containing a rich fauna. In places where the rock is of irregular formation, such as at Omoa in Fatu Hiva, the shelf is much hollowed and undermined, and blow-holes, from which the surf throws columns and spurts of spray, are characteristic of many coasts, as they are in the Cape Verdes.

The algal flora is of the usual tropical type, of numerous species but inconspicuous quantities. The masses of *Sargassum* and abundance of other weeds which characterise the Galapagos are not found here, but neither are the shores weedless as in Panama. Lithothamnion is alone conspicuous; the lower part of the shelf below the cliff is often whitened by a thin coat of dead Lithothamnion, probably dried this season when the surf is less on the

\* AGASSIZ, A., "Albatross Tropical Pacific Expedition," *Mem. Mus. Comp. Zool. Harvard*, vol. xxviii, 1903, p. 4; also *Bulletin*, vol. xxiii, No. 1, 1892 (Galapagos, etc.).

† CROSSLAND, C., *Journ. Linn. Soc.*, vol. xxxi, and *Desert and Sea Gardens of the Red Sea*, Cambridge University Press, 1913.

sides of the island we visited, but between tide-marks is a thicker crust of the usual pinkish purple. This is rarely, or never, of Lithothamnion alone, generally it is combined with the Serpulid *Bispira*, which, though inconspicuous, may in some cases form the greater part of the mass. Or a *Vermetus* may be present as in the incrustation of the Cape Verde Islands, but a minute species, 1 mm. in diameter. This incrustation is thickest near the lowest point exposed by the retreat of a wave (the tide is trifling compared to the rise and fall of the surf, even on the leeward side of the islands), but it extends beyond low-water level. Where this covering fails some other organism takes its place, there is no square foot anywhere below high tide which has not its organic carpet. Areas of many square yards are covered with rubber-like sheets of Zoanthid Actinians, a slaty coloured form with bright green tentacles being the most common, a dull yellow with larger polyps being also abundant. Soft weeds are rare, but *Halimeda*, which had not been seen since we were at Colón, occurs in the pools of the shelf. Below lowest tide-level the covering may be of yellow sheets of *Millepora*, which, within the bays, sends up abortive branches only 2-4 inches high, and is often purely encrusting. Other areas may be completely covered by a small flat shell, *Anomia*, hidden under a thin coat of Lithothamnion. Corals are not uncommon, being exposed on the retreat of a wave and extending below this level for several fathoms. The principal coral species are two of *Pocillopora*, of forms obviously different from those of Panama, and one *Porites*. All have peculiar growth forms, occasionally in the case of the former, generally in the latter, which indicate local adverse conditions, probably the rasping action of the sharp sand which is characteristic of these inlets. Thus a large dark brown species of *Pocillopora* with broad branches may occur as regularly branching colonies, or the branches may be flattened into plates placed parallel to one another, or a remarkable form may be assumed in which the long side branches creep almost horizontally over the substratum, the central ones which should grow upwards being aborted, thus giving to the whole the appearance of a giant lichen; this may occur on both vertical and horizontal faces of the rocks (see figs. 2 and 3 on Plate). Another abundant *Pocillopora* has more slender branches and is of a light yellow-brown colour, the colonies forming hemispheres of closely packed branches about the size of the first species; a third species resembles the normal form of No. 1, but is a uniform dark green in colour, and is rare (Plate, fig. 4). The strange inverted cone form of *Porites* (Plate, fig. 1), which is a common and characteristic coral of the Marquesas, and quite new in my experience, was first seen just outside Taa Hu Ku Bay. On sending down a diver for what appeared to be a vase-shaped *Turbinaria*, or such plate-like coral, what was my astonishment to see him struggling with a solid, heavy mass and produce a *Porites*. Such a thing was utterly unknown in my previous experience, but Professor GARDINER tells me that he has seen it once, on a muddy bank on the Chagos bank in the Indian Ocean. It is evident that this form is assumed in consequence of the rasping action of the sharp sand, just as the corymbose (stalked) bouquet-like species of *Madrepora*, gain the immense advantage of support above the sea bottom, a point which is further discussed in my account of the reefs of Tahiti.

Arakei Island, off Atuona, was explored in the hope of finding more flourishing coral growth away from possible detrimental influences from land, but even here corals never cover the bottom, and only the same species are to be seen. The yellow *Millepora*, however, reaches a further development, sending up spatulate branches a foot or so high, and becoming the facies known as *M. truncata*. This may again develop into another facies, in which large, flat, vertical branches are set into a rough honeycomb, the cells of the "combs" being, say, 4 inches across, and in other localities this form makes masses of great size which are important constituents



of certain reefs. All, as HICKSON suggested, belong to the same species in spite of these apparently wide differences (Plate, figs. 5 and 6 and legend).\*

Other species were found about Taa Hu Ku only as rarities, *Porites* lichen forms small thin incrustations in shore pools, combined with the same Serpulid *Bispira* as occurs in the lithothamnion crust over the rocks and is found only in such combinations, and a massive *Porites*, common in other places, was seen only once here. A third species was found only in a pool on the broader shore shelf near Atuona, as a low, flat-topped cylinder, so much decayed in the centre that the living part forms a sector of a ring on one side; this has resumed growth on the inner side of the ring. Near this is a series of small hemispherical colonies of the same species, apparently independent but set in a circle in a way that shows their origin to have been from a cylinder like that just described, the centre of which has wholly disappeared, leaving portions like that on the side of the first specimen, which have resumed growth as independent colonies. These details are given as illustrating the fact, which the whole investigation of the coral fauna will emphasise, that not only is the fauna restricted beyond all hope of any normal reef formation, but also that half the fauna is here but as a remnant struggling against adverse conditions. This is due not so much to the failure of species to reach these, the outermost of the Pacific Islands, as to the impossibility many species find in establishing themselves. The same thing applies to the other groups of which collections were made.

The bottom of the bays, like the beaches at their heads, are nearly barren. They are floored with a black sand of a clean, sharp character. The dredge brought up nothing but some small Prosobranch mollusca, an *Anomia*, and masses of the gelatinous polyzoan *Zoo-botryon*, no weeds, corals, large shells, or stones. It is difficult to account for the coral material after the death of the polyps, none being incorporated into the beach; presumably some reaches the bottom of the rocks where it may be rapidly buried in sand, but the absence of visible deposits is striking after their comparative abundance in Panama, where growth is no more vigorous and the number of species still less.

Other beaches do contain some coral. At Hana Iapu on the other and windward side of Hiva Oa, CHUBB found corals thrown up in sufficient quantity to form a considerable proportion of the beach, and his specimens show that the corals are the same as on the south side, but that that funnel-shaped *Porites* is present in quantity. At Omoa, in Fatu Hiva, there is no coral on the main beach, a little on the boulder beach to the south-west, and a considerable amount on the beach of finer material under a big cliff farther on in the same direction. Here half the mass of the upper part of the beach is coral, still hard, not at all rotten, and so much rolled that the growth forms cannot be distinguished. The largest piece of *Porites* was about 2 feet across, containing *Saxicava* burrows of exceptional size, exposed by the removal of several inches of the whole surface of the coral.

In Omoa Bay itself there is a conglomerate of rolled boulders at a level of 6-8 feet above tide-mark, the cement of which contains Lithothamnion with *Vermetus* tubes, this being the only place where an elevated beach was seen, though other possible occurrences were heard of. In a little bay northwards from Omoa Mr CHUBB found considerable quantities of coral thrown on to the rocky shore shelf, some pieces being 2-4 feet in diameter.

Most of the valleys are too wet to allow the formation of beach rock at their mouths, but deposits were found in dryer valley mouths, such as Vai Tahu ("Resolution Bay"), Motopu, and Hapatoni, in Tahuata Island. At Vai Tahu the beach does not dam the stream, the ground behind it sloping gently upwards, and a hole dug 30 yards inland exposed beach

\* HICKSON, S. J., *Proc. Zool. Soc.*, 1898, p. 246, and WILLEY's *Zoological Results*, Cambridge University Press, 1902, p. 121.

material, including coral. The stream is small and was practically dry, though there had been heavy rain in the night, and the village water-supply is from a spring in the face of the cliff on the south side of the beach. The sand contains a higher proportion of shell and coral than usual. Beach sandstone flats are found at low water, a small patch on the north side of the northern beach, while the whole of the south beach has a flat beneath it which extends out under water, giving the bay a strangely regular and almost smooth bottom of clean rock, in deeper water ending in tongues with shallow fissures between them. Coral is abundant, the big brown *Pocillopora* in regularly shaped colonies, *Porites* both the brown funnel shaped and the rounded whitish species, with honeycomb like masses of *Millepora* almost covering the bottom. It is evident how little more coral accumulation, either by increased growth or less active destruction, would convert this into a reef. It was here too that the gradations between the funnel-shaped *Porites* and the usual dome shape, as sketched in fig. 9, were first seen. The last stage is in growths 12-18 inches each way, but these lead directly to the great heads of Controller Bay and Tai O Hae, in Nuka Hiva Island, in the northern division of the group.

Controller Bay is the deepest and most fjord-like in the group, and is, according to CHUBB, the submerged part of the moat between inner and outer volcanic cones. Its divisions, and the little living coral deposits, are shown on the map (fig. 8). They are peculiar through the development of the *Porites* sketched in fig. 9 into great heads, comparable to those common in coral seas, measuring 6 feet each way. Nearly all appear to be young, having their tops dome-shaped, not flattened by reaching the surface. It is also remarkable that the ordinary forms of this species, such as figs. 1 to 4 of the series, are not present, and there are very few small colonies such as fig. 5. This illustrates the general fact in coral ecology, that the settlement and survival of coral larvæ occurs but rarely, only under special conditions can a reef be founded, though its growth may go on when those special conditions have passed. The whitish *Porites*, which has such a phenomenal development at Hana Hevané, the climax of reef formation in the Marquesas, also occurs here, but does not form any considerable part of the flat, and the other forms and species are all present, the big brown and green *Pocilloporas* being the most abundant, with two other species not seen before. In addition a species

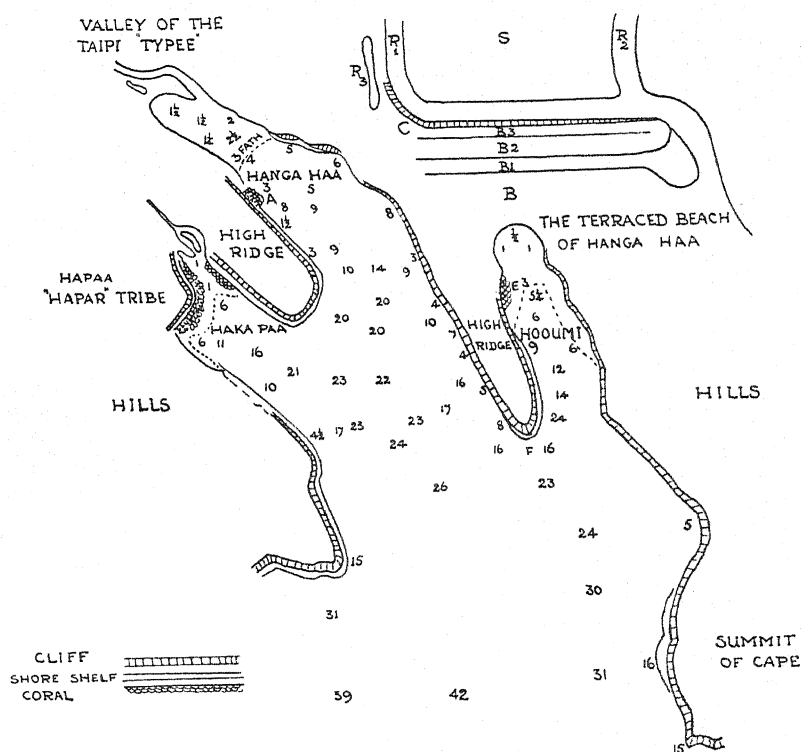


FIG. 8.—Controller Bay, in Nukuhiva, the submerged end of the moat between the two cones of the island, showing the distribution of the cliffs, shore shelf, and coral deposits. Inset the beach of Hanga Haa, which rises in three terraces, is cliffed by the river inland, and shows three old channels: R1, the present; R2, that of the chart of 1844; R3, still older. B, the present beach; B1, recent but covered with *Ipomoea* and temporary vegetation; while B2 and B3 are higher and planted with coconuts, which, however, are falling over the cliff into the river behind. S is a swamp of "Purao" *Hibiscus (Paritium) tiliaceus*.

of *Montipora* is abundant in this bay, and only here. *Millepora* is less abundant than usual, but generally forms masses rivalling those of *Porites*, a development also found in Tai O Hae Bay. At the point marked by an arrow the big *Porites* heads stand alone, but southwards is a continuous flat, without a raised edge. This is composed of large dead branches of *Pocillopora*, some of them in position of growth, with a few small living colonies, and in places

the outer slope is similar. *Lithothamnium* are abundant, though not so conspicuous as on the shore shelf, forming loose nodules with pieces of coral as nucleus, or exceptionally a pebble of basalt; the coral *Psammocora* forms rather similar pieces. The *Lithothamnium* here again fail in their rôle of cement and there is no *Polytrema*, etc., to assist, nor do sponges and ascidians, which in many reefs help to keep loose materials together. The reef gradually tails off southward into a flat with 2 to 3 fathoms of water over it, covered with corals and their debris; lava boulders soon appear, and it is evident that the deposit is only 12 to 18 feet thick, built upon a shelf at about this depth. The other patches, *b*, *c*, and *e*, were all visited and their coral origin verified; all are essentially like the first. The whole bay was searched for other occurrences by paddling round its shores with a water-glass, a slow method, but one insuring that no detail shall be missed. On reef *c* were found the only specimens of *Fungia* seen in the Marquesas.

Coral growth on these patches is abundant, but not more so than at other places where no reef has resulted, and clearly these reefs exist rather through the preservation of the dead coral than to any exceptional vigour of its growth.

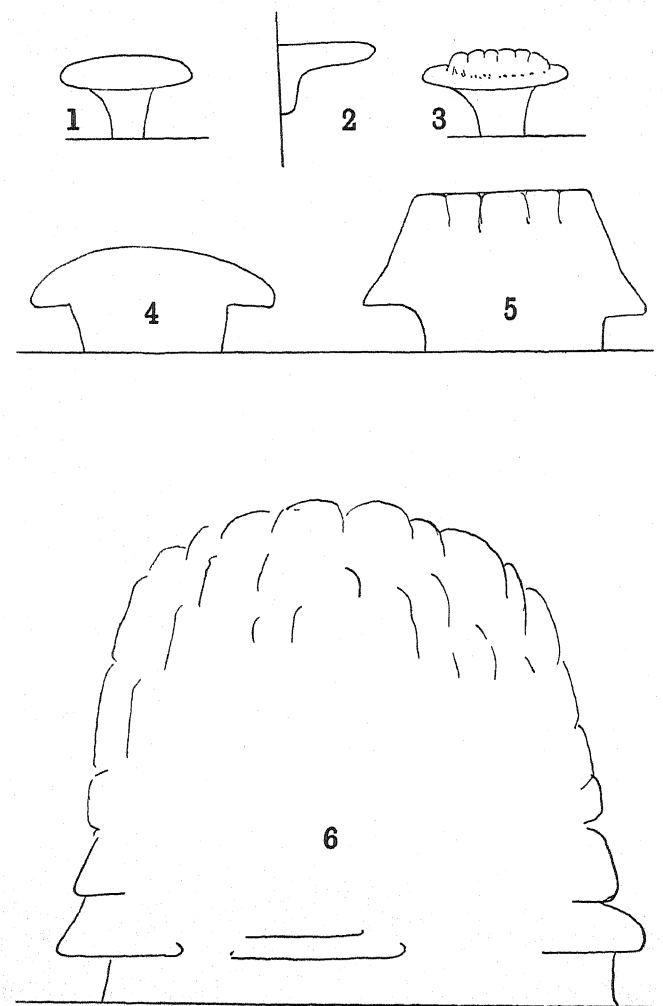


FIG. 9.—Marquesan *Porites*. Diagrams of the stages between the funnel-shaped form and the large cylindrical head. (1) The funnel form, typical of localities of restricted growth; (2) The same on a vertical rock; (3) Rudimentary upward growth; (4) and (5) Stages leading to the fully formed cylindrical head (6) found in Controller Bay and Tai O Hae.

All the reefs occur on the west side of the bays. Not only are there no patches, however small, on the east side of Hanga Haa, but coral is comparatively scarce and its debris seems to be completely removed. Apparently suitable foundations for reefs are present all along the shore, but *Millepora* alone has been successful in covering the rounded boulders, and this is poorly developed, only occasionally sending up ill-developed branches. At the end of the point *f* conditions seem ideal for coral, the visibility extending to 5 fathoms as against  $1\frac{1}{2}$  to 2 at numerous points inside the bay, but they are no better developed here. Near the head of Huumi Bay is a little break in the cliffs and a beach recalling that at *c* in Haka Paa, and here there is a small reef, but more submerged and less regular at the edge, which is marked by big heads of *Porites*.



The bottom of Hanga Haa seems to be exactly like that of Taa Hu Ku, *i.e.* fine volcanic sand with very little life. A large bucketful of muddy sand was passed through a fine sieve and gave a small spoonful of broken shell, and not a single worm. By keeping the trawl more on the surface a mass of *Zoobotryon*, some small prosobranch molluscs, and *Anomura*, were obtained exactly as at Taa Hu Ku.

Very similar coral banks were found in Tai O Hae Bay,\* but the coral flat definitely inserted on the chart of 1844 no longer exists. There are massive heads of *Porites*, mostly dead or half-dead, and bearing quantities of *Halimeda* and some *Pocillopora*. The other corals present are *Pocillopora* 1, both normal and palmate forms, with Nos. 2 and 5 of the list below, *Montipora* in sheets only, without the upper fan-like portions seen in Controller Bay, and *Millepora* in large masses, which, like the *Porites*, are often dead. There are clear indications that a coral flat did exist here at the time the chart was made, vindicating the extreme accuracy with which French surveyors worked in all their oceanic establishments, but it has collapsed through undermining, the bottom being covered with masses of flat rock, lying at an angle with the horizontal. Ashore is a quantity of conglomerate in the same condition formed of a mixture of volcanic sand and pebbles, coral, and shells. There is more growing coral on the east side of the bay, but no reef, nor trace of one having existed. I learned of patches in the adjacent Tai Oa Bay quite similar to the above from Col. KELSALL and Mr CHUBB.

The shore pools of Tai O Hae Bay were found to be extraordinarily rich in comparison with localities previously seen in these islands. Hydroids and Polyzoa, for instance, had been practically absent hitherto, yet here were several species in abundance, particularly a *Pennaria* which covered much of the area of many pools, and which, in appearance at least, seems to be the same as that found in all my collections. The Opisthobranch mollusca are usually collected species by species, often with long intervals between each find, yet here no fewer than *nine* species were collected from one pool, followed by others on succeeding days. This had struck me as a phenomenal occurrence in the Galapagos with their rich continental fauna, but it is much more significant when met in these most isolated of oceanic islands. The usual difficulty in getting a canoe-man here was overcome for me by Colonel KELSALL's volunteering to dive for corals and weed. A quantity of *Halimeda*, from one of the *Porites* heads, gave an interesting fauna of green animals, a small crab, an amphipod, a little *Elysia* (*Sassoglossa*, Nudibranch), green as usual but *without* the characteristic coloured border, and a *Cæloplana*. The crab carries *Halimeda* leaflets, but its body is bright green also, and is flattened, so that it matches the *Halimeda* in shape as well as colour. Other members of the fauna were not green.

The largest coral growth in the Marquesas is found at Hana Hevané on the north-east coast of Tahuata near the west end of the straits between this island and Hiva Oa. Its geographical position gives it shelter, and the character of the adjacent land shows that interference with coral growth by fresh water is at a minimum; at Omoa, too, it was noted that the valley above the possibly incipient, possibly reduced, coral deposit was dryer than usual. This part of Tahuata Island is so dry as to be almost desert, only the valley mouths being productive, and the oases they make are poor in comparison with the richness we had come to associate with Marquesan valleys. The hills are low and comparatively tame, the scenery and coast recalling the south of Fifeshire, but the bare hills are not green with grass but with a succulent edible plant which appears in places in the Red Sea deserts after rain. Both at

\* I owe the opportunity of examining these, and the large additions to my collections made here, to the very kind hospitality of the Rev. Père Siméon Delmas, whose large collection of Mollusca corroborates the contention that prolonged work here might modify our views on geographical distribution in oceanic islands.

Hana Hevané and the more extensive bay at Motopu the stream only flows after rains, the inhabitants of the latter, and the solitary guardian of the coconuts at the former, being dependent on springs, that at Hana Hevané being on the seashore and only accessible when the tide is half down.

Three of us stayed with our solitary friend (an elderly Tuamotuan named PASCAL, a gentleman already celebrated in some of the romantic South Sea tales), and so made a detailed examination of the reef.

The reef stretches across a little bay, well within the heads, and encloses the inner part of the bay as lagoon, 2 fathoms deep and small in proportion to the width of the reef. It is broken by a canal-like passage near the north side, 2 fathoms deep seawards, 1 lagoonwards; the outer slope is gradual, descending to the bottom of the bay, which is 5 fathoms deep at its mouth. The surface exposed at low tide is broad, but the whole has grown at its present level, there has been no planing down by the sea. In places settlement has opened cracks, and near the edge are spaces not yet filled in, and these are bordered by new growth of *Porites*. A broad band of stones occupies the highest part of the flat, the larger of coral, the smaller being volcanic boulders. The former are irregularly weathered, not rounded like those found on the beaches, black, and covered with small angularities like the stones found on the reef edge of Zanzibar, but distinguished from them at the first stroke of the hammer, the latter being very hard remnants of recrystallised elevated coral, these being unaltered *Porites* which recently grew on the reef edge. They reached their present position as the result of quite abnormal weather, none being found which had not lain here for years. On the inner side banks of *Pocillopora* branches, on the surface at least loose and uncemented, slope into the lagoon. The small volcanic boulders are not part of an underlying spit forming the foundation of the reef, but all lie upon the coral to which they are organically cemented, and into which they may be more or less sunk. They are derived from the beach, from which they have travelled over the coral more or less at right angles on the shore, a phenomenon probably of more importance on other reefs, e.g. those of Tahiti.

The main mass is composed of *Porites* 2A, with additions due to a plentiful growth of *Pocillopora* upon its outer slopes. This *Porites* does not grow as a collection of isolated heads, but as a continuous mass, and may possibly be one enormous colony, yet another novelty of coral growth to add to the list of novelties collected on the voyage of the *St George*. *Porites* No. 1, it is strange to find, does not occur. At either side of the bay the flat begins as a narrow band of this *Porites*, which forms a continuous surface and falls vertically into a fathom or so of water at its edge. There are numerous loose nodules of *Lithothamnium* and *Psammocora* on the dead part of this flat, and seawards other corals appear, and large colonies of yellow *Millepora* decorate the edge, especially of the channel on the west side, growing in rounded masses made of thin plates, which are coated with *Lithothamnium* from a little below their edges to their bases. Seawards *Pocillopora* abounds, the species being Nos. 1 and 2 in their normal forms, the pink variety of the latter being common. There is no raised edge, and the outer slope is gradual, richly covered with corals of the few species mentioned. Serpulids are not seen in masses, but are abundant on both corals and *Millepora*, where these are overgrown by *Lithothamnium*, but outside the bay the Serpulid-*Lithothamnium* incrustation and the general fauna are developed as elsewhere.

The little islets to the extreme north-west of the group (not shown in my copy of the chart) generally described as "the only coral islands in the Marquesas." It was impossible for the *St George* to go far out of her course as to visit these isolated, and otherwise uninteresting, banks, but it is to be noted that the French charts name them "îles de Sable,"

which is probably the correct description. The captain of an island schooner told me that they are mere sandbanks which may disappear in bad weather, reappearing after normal winds have prevailed for a time.

These reefs, which certainly are not comparable to coral reefs elsewhere, have been described at inordinate length, partly on account of the controversies and theories which have been written on the corals of the Marquesas without any account of what actually is there, and because they seem to the writer to afford interesting problems in ecology, and a simplified case of coral formation which may possibly at some time throw light on wider questions.

In spite of the restriction of the coral fauna the balance may turn to accumulation under special conditions, the chief of which, as shown by the distribution of such rudiments as occur, are shelter and the absence of fresh water. Had, however, such conditions been more frequent in the group, leading to extensive deposits in place of the patches actually found, we should be no nearer to the formation of real reefs, which, as DAVIS points out, must be able to resist the ocean surf. Indeed these patches generally owe their preservation to the protection afforded by growth of massive *Porites*, which, in spite of its weight and solidity, in all seas is an inhabitant of sheltered water. It is evident that cementing organisms are essential to the formation of a surf-resisting reef, and in these islands, where they exist, they fail in their binding action. The reef at Hana Hevané is unique, and is simply a phenomenal growth of a species of *Porites*, to which the other corals are entirely subsidiary. It is possible that the whole structure is one colony and owes its existence to a single ovum. There is perhaps significance in the fact that the coral fauna of the northern islands in latitude  $9^{\circ} 0' S.$  is richer than that of the southern, which are between  $9^{\circ} 40'$  and  $10^{\circ} 30' S.$

The total coral fauna of the Marquesas, being of peculiar interest in respect to reef formation and to geographical distribution, may be summarised. The species are indicated by numbers, as BERNARD did in his British Museum Catalogues, the corals, with the exception of *Fungia*, belonging to genera which have not yet been determined as to species by monographs on modern methods.

*Pocillopora*.—Sp. 1. Dark chocolate brown, ends of branches whitish or pink. Branches thick and colonies large, 2 or even 3 feet across. The species grows in three forms, (a) normal, branches forming a regularly shaped growth, (b) with branches broadened and flattened abnormally at their ends and placed parallel to one another, (c) the "lichen" form, in which the outer branches are applied to the substratum and the vertical fail to develop (Plate, figs. 2 and 3).

Sp. 2. With more delicate branches, light yellow-brown in colour. Colonies under a foot in diameter, close growing. There is also a similarly growing bright pink form which I interpret as a colour variation.

Sp. 3. Very small, delicate, pink in colour. Seen only once, in a shore pool at Vai Tahu.

Sp. 4. Like (1) but dark green in colour. Possibly only a colour-variety of (1), but the branches are longer in proportion and looser in arrangement (Plate, fig. 4).

Sp. 5. With the swollen ends of the branches bearing long spine-like processes (seen only once).

*Porites*.—Sp. 1. The form illustrated on Plate, fig. 1, and text-fig. 9 as varying in mode of growth from small inverted cones to great cylindrical heads. Colour brown or yellow-brown.



*Porites*.—Sp. 2. Colour whitish or grey, forming rounded masses, generally resembling small boulders.

Sp. 2A. The species of the reef of Hana Hevané, whether distinct from the preceding or not, was not decided. The surface is bluish white but the shaded parts are brown.

Sp. 3. *Porites lichen*. As thin incrustation only, sometimes with pointed projections. Colour greenish or yellow-brown.

*Psammocora*.—Only one species, as loose nodules, rare.

*Montipora*.—One species only, in sheets, sometimes with upper fan-like sheets above the one incrusting the rocks. Colour brown, upper surface spiny. Distribution local.

*Fungia*.—Four small specimens only were seen, and those at one place.

There may be also an *Astrean*, occurring as small incrustations, but as no specimen was secured this remains doubtful.

The whole coral fauna thus consists of four or five species of *Pocillopora*, three or four of *Porites*, and one each of *Psammocora*, *Montipora*, and *Fungia*, only five genera, a complete contrast to other coral seas. Further, of these few species only five are of any importance, viz. *Pocillopora* 1 and 2, *Porites* 1, 2, and 2A, and of the remainder *Pocillopora* 4 and *Porites* 3 are fairly common, but do not add to any of the accumulations seen, the *Montipora* is abundant, but only present at all in two localities, while *Pocilloporas* 3 and 5, the *Psammocora*, and the *Fungia* are rarities, i.e. five out of the ten or twelve have succeeded in obtaining a foothold and no more. The whole immense genus *Acropora* (*Madrepora*), one of the chief of reef builders in modern seas, and of the first importance in the Society Islands especially, is entirely absent, the *Astreans* are possibly present as one insignificant remnant, *Galaxea*, *Mussa*, and all its allies, besides all the hosts of less abundant genera, are not to be found. The *Alcyonaria* too are absent, both fleshy and hard forms, including that almost universal constituent of a coral fauna, *Tubipora*. The fact that half of the species present are here, but as rarities, suggests that the poverty of the fauna is due as much to adverse conditions as to the isolation of these islands in the ocean, a supposition which receives further support from the coral fauna of Tahiti. One adverse condition is certainly the rasping motion of the sharp sand over the bottom, which effectually prevents the settlement of larvæ. Its effect is shown also in the abundance, in the southern islands, of the funnel-shaped *Porites*, this form having been evolved to support the bulk of the colony above this destructive action, just as has the stalked or the corymbose group of species of *Acropora*. At Vai Tahu the numerous small colonies of this form of *Porites* indicates a periodic destruction of the corals and of their dead remains. The abundance of *Millepora* and its form of growth is another indication of the effect of sand, since two localities in Tahiti, to be described later, clearly show that *Millepora* is the last survivor when the reef corals are destroyed. As regards temperature many more observations are necessary, as an occasional fall might have the same effect upon corals as a permanent difference. The temperatures of the surface waters between the islands were between 26.6° and 27.2° C., and beyond Napuka Atoll, 27.7° C., differences probably of not much significance.

Napuka Atoll with another named Tepoto, are distant outliers of the Tuamotu Archipelago to the north-east. It is described by the "Sailing directions" as the most primitive of the group, the inhabitants still being only partially clothed and living upon dogs and the fruit of the *Pandanus*.

We found that the atoll has been taken over by a commercial company of Tahiti and planted with coconuts, the natives supplied with pigs and the blue trousers inseparable from

French civilisation. The people are not Tuamotuans but Marquesans, the descendants of the crew and passengers of a big canoe which was blown out to sea, and was one of the lucky ones which found, and colonised, yet another of the Pacific Islands.

As the outline chart shows, the atoll is somewhat triangular in shape, containing a lagoon into which there is no opening. The islands are reduced to sandbanks on the windward side, elsewhere they are 12 to 15 feet high, with white coral beaches, above which the surface is composed of dark grey clinker-like pieces of coral. The reef is awash between the islands, and bears numerous masses of reef rock. The lagoon is shallow and full of shoals, which are stated in the sailing directions to project above water as rocks. We found those which we were able to see to be covered with "Stags' Horn" *Acropora*, but the rocks, which we had hoped to find so interesting, were merely heaps of *Tridacna* shells, the flesh of which had been used for food. We had time to explore only the western (*i.e.* leeward) of the islands. On landing, the narrowness of the reef and its flatness, *i.e.* the absence of any hollowing out into a channel, impressed me as striking differences to any I had seen. The reef here is a mere step, about 20 yards wide, and it does not exceed 50 yards in width anywhere along this island except at its ends; in other words the land has covered the reef practically to its edge. There is no coral on the reef flat except *Porites lichen*, as thin crusts which are easily detached, and are often found on the beach. There are a few small colonies of *Pocillopora* on the outlying buttresses, and lithothamnion is present in quantity only on these, and in the furrows of the reef edge. The flat itself is of a bright pink colour, but this is due to a small red confervoid weed. The flat is due to erosion, its rock is hard and smooth, and in places shows corals in section in its surface. The furrows are due to erosion, they are not spaces between outgrowing

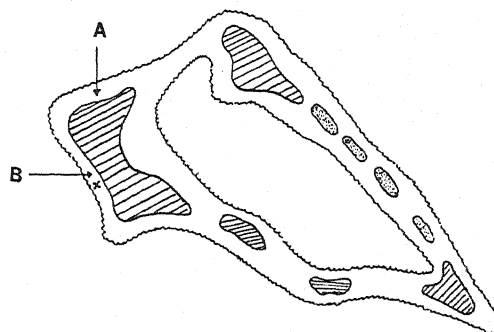


FIG. 10.—Napuka Atoll. Island shaded, sandbanks dotted. The lagoon is shallow and full of shoals not charted. A and B, points referred to in the text. X, landing place.

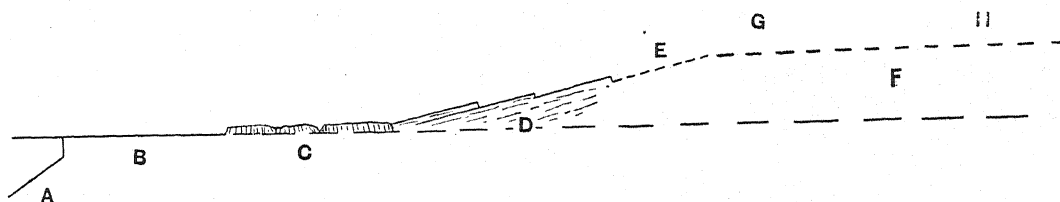


FIG. 11.—Diagrammatic section of the reef and beach of Napuka Atoll. A, the coral-covered slope; B, the barren erosion flat; C, the higher flat, planed off when sea-level was higher; D, slabs of beach sandstone; E, loose coral and sand; G, Xerophytic coral beach flora; F, the island, composed of coral "clinkers" bearing coco-palms at H. Reef-rocks thrown up by storms not shown.

tongues, and the edge often overhangs, to which undermining may be attributed the numbers of slabs of coral rock thrown up on to the reef. The corals in these are in position of growth relatively to one another, but the whole is overturned; the larger pieces may measure  $10 \times 6 \times 4$  feet high. Remains of an original flat from which this is being eroded are to be seen around the point marked A at a height of 1 or 2 feet above that of the present flat as shown in the diagrammatic section of fig. 11, and another exposure at about the same level exists in a depression in the southern end of the island near the lagoon. These indicate a pause in the lowering of the ocean surface, during which an elevated reef was planed completely down, leaving no traces here such as have been described by DANA in other atolls of the group.

There are large quantities of beach sandstone between the points A and B, great slabs covering the beach as in the sketch. Some of the lower layers of the rock show the grooving made by rain, the grooves passing under the next layer above, indicating the removal of overlying material and the formation of fresh strata. We have here the typical conditions for this rock, viz. seepage from the land in place of running water, this seepage being already charged with  $\text{CaCO}_3$  and  $\text{CO}_2$ , and the above observation shows that the consolidation of the beach takes place in a shallow surface layer over already formed and generally impervious rock, as is described by GARDINER in *The Fauna and Geography of the Maldive and Laccadive Archipelagos*.

The origin of the abundant coral debris which forms the beach and island is the slope below the cliff of one or two fathoms of the reef edge, which is covered with living corals as far down as I could see. It reaches the beach only in exceptional weather, in northerly or westerly storms. The south-east trade was blowing a gale at the time of our visit, but the surf merely flooded the flat and lapped the base of the beach.

To the lagoon side the island descends in a gradual slope, becoming more sandy until the lagoon shore is completely of sand. There is no beach, and no distinction between the island and lagoon flat but the cessation of vegetation, and an almost imperceptible rise of level in the sand was occupied by vegetation forming a little island—it is evident that accumulation is in progress here, and the vegetation is extending slowly into the lagoon, while the shallowness of the lagoon and the number of shoals in it indicate that it is filling up.

The south end of this island has been formed more recently, and shows a succession of distinct beach summits as ridges parallel to the shore, which are of interest in showing stages in the formation of the cinder-like coral shingle which make the mass of the island. The newer beach is formed of coral branches in which the effect of solution by rain is very evident, all the smaller branches, with much of the surface of the larger, being removed, yet leaving the shape of the coral recognisable. In the older beaches, where the process has gone farther, it is less evident that it is the result of simple solution, as the pieces have become so altered that, without the evidence of the earlier stages, other causes for the effect might be given. That this process is a very slow one, while the consolidation of beach conglomerate is rapid, will be shown in my description of Tahiti.

I wish to thank the Managers of the Balfour Fund of the University of Cambridge for enabling me to buy the collecting apparatus used, and several firms for presenting to the owners of the S.Y. *St George*, bottles, jars, and reagents, of which I was the principal user. The spirit was provided by the British Museum.

#### EXPLANATION OF PLATE.

##### MARQUESAN CORALS.

Fig. 1. The funnel-shaped *Porites* characteristic of the southern group of these islands. This specimen 14 inches across the disc.

Fig. 2. The "lichen form" of the brown *Pocillopora*, with long horizontal branches and aborted central branches. Length 18 inches.

Fig. 3. *Pocillopora* 1 with flattened parallel branches. In this specimen some are overgrown with a lithothamnion at the ends, the black dots in which are the openings of *Vermetus* tubes. 12 inches across.

Fig. 4. The green form of ? *Pocillopora*.

Fig. 5. *Millepora* of the facies *truncata*. Abundant in the Marquesas, but this specimen is from Tahiti, where it was the only one seen. Scale in inches.

Fig. 6. *Millepora* of the honeycomb facies. This specimen 14 inches across.



Dr CYRIL CROSSLAND on "Marine Ecology and Coral Formations in the Panama Region, etc."—PLATE.

